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THE BIOLOGICAL WORLD

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MAN
AND
THE BIOLOGICAL WORLD

BY

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MAN AND THE BIOLOGICAL WORLD

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Preface

The past ten years have witnessed the introduction of numerous survey courses in the various sciences. Such courses owe their development to the feeling that the usual freshman course of a particular discipline is at once too technical and too limited for the student who desires a general cultural knowledge of the subject rather than a professional training. Although nearly all educators will agree that some appreciation of the findings and problems of the biological sciences should form a part of a liberal education, the great majority of college students cannot afford time for more than a single course in this field. For them some integrated account of the contributions that biology has made to man's understanding of himself and his environment seems more pertinent than the more detailed and more restricted preparation for the advanced courses they will not take.

If it be granted that a survey course has a place, the question of what viewpoints and what subject matter can and should be presented still remains. The authors are part of a group that was requested to organize a "comprehensive" or "survey" course in the biological sciences for underclassmen at the University of Florida. Now, after some six years of experiment with and modification of subject matter and presentation, with classes of first- or second-year students, they are convinced that a presentation of biological principles that stresses an appreciation of the data and reasoning on which such principles are based is practicable as a single-year course and provides a definite contribution to the student's knowledge of himself and of the world in which he lives.

In order to adapt the survey course to the needs of those students who decide to major or take further work in biology at the University of Florida, laboratory courses that more or less parallel Part I of this book are elective in biology.

It is impossible for the authors to acknowledge all of their indebtedness to other biologists. Perhaps it is not inappropriate to quote from Kipling's introduction to *Barrack Room Ballads:*

When 'Omer smote 'is bloomin' lyre,
  He'd 'eard men sing by land an' sea;
An' what he thought 'e might require,
  'E went an' took—the same as me!

The authors are grateful to the various publishers and to the General Biological Supply Company whose loans of figures are specifically acknowledged under the reproductions of the illustrations in question. They are greatly indebted to Messrs. Joseph C. Moore and William Brudon, students in the Department of Biology, and to Dr. Albert M. Laessle, instructional staff, University of Florida, for the original drawings and diagrams. Gratitude is expressed also to Prof. A. E. Hooton, of Harvard University, who very kindly read and commented on the preliminary draft of Chaps. XXXI and XXXII; to Prof. A. F. Shull, of the University of Michigan, both for reading an earlier draft of the entire manuscript and for his courses and publications; to Dr. Georg Neumann, of Indiana University, for assistance in preparing Chap. XXXIII; and to the authors' colleagues in developing and teaching Man and the Biological World at the University of Florida—Prof. H. B. Sherman and Drs. A. F. Carr, H. H. Hobbs, and H. K. Wallace—who have provided many pertinent suggestions and criticisms. Finally the authors wish to acknowledge the unvarying cooperation of Dean W. W. Little, of the General College of the University of Florida, and the freedom he has granted and maintained for them in choosing the viewpoints and materials for the biological part of a "General College" curriculum.

J. Speed Rogers,
T. H. Hubbell,
C. Francis Byers.

Gainesville, Fla.,
October, 1942.

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CHAPTER I

Introduction: The Field and Problems of Biology

WHATEVER else man may be—a rational, a social, or a religious being—he is also a living organism. Along with a million or more of other kinds of living things, he is composed of the intricate stuff called *protoplasm* and is subject to the peculiar laws that govern its existence and functioning. Underlying such aspects and principles of human conduct as are the special concern of history, sociology, and economics are fundamental attributes, capacities, and limitations that are inherent in man's organic make-up and his membership in the domain of living things. The present book is concerned with some of the basic principles that have been found to apply to this world of living things and that help us better to understand ourselves and the world in which we live.

The field of knowledge that concerns itself primarily with life processes and living things, as such, is known as *biology.*[1] This science seeks to discover and describe all the phenomena concerned with living things and the state of being alive, and has amassed a huge content of facts, hypotheses, and principles that give us an insight into man's existence, limitations, and potentialities. Even if our only interest in biology were to obtain a knowledge of the principles that govern human existence and welfare, we could not profitably or efficiently confine our attention to man. He is one of the most complex of all organisms, unavailable for many kinds of experiment and observation, with much of his biological make-up modified or concealed by his intellectual and social attainments. Abundant experience has shown that most of our surest knowledge of the biological principles that apply to man has been gained, and can best be tested, by turning to other forms of life that are more available for experiment and safer for objective observation. Indeed, much of man's biological heritage and background is best understood from some appreciation of the whole living world in which he lives, of which he is a part, and which he must in some measure control and exploit.

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[1] The word "biology" comes from two Greek words: *bios*, meaning "life," and *logos*, which literally meant "the word," "a discourse," or "the discussion of," and has come to mean "the science of."

We can obtain a concrete idea of the scope and content of biology and the light it can throw on many aspects of human function and behavior if we look at some of the important problems that are met with when we attempt to comprehend a single living organism. Whether we look at man, at one of the familiar animals or plants he has domesticated, or at one of the innumerable but less familiar "wild" forms that live all about us, we shall encounter a series of broader and broader problems as we examine our selected organism from various points of view.

The Organism as an Isolated Individual. When we inspect any organism from the simplest possible viewpoint, as an isolated individual, without question as to its origin or possible relations to other individuals, it still presents two closely related problems: "How is it constructed?" and "How does it work?" Neither question, as yet, has been completely answered for even the most familiar organism, but the partial answers that have been obtained form a large part of the subject matter of biology and are fundamental to any understanding and appreciation of the still more complicated problems of organic interrelationships.

The answer to the query, "How is this individual constructed?" will be found to necessitate an analysis of its component parts. Scrutiny of its outwardly discernible form and structure will show it to be made up of diverse parts, and these, together with a variety of concealed but equally gross internal structures, will be found to be fabricated from smaller parts, and these, in turn, from still smaller, until the analysis reaches the limits of microscopic detail. Similarly, the attempt to discover "how it works" reveals the same high degree of organization. Such major processes as motion and locomotion, digestion, respiration, coordination, and appropriate behavior resolve themselves, step by step, into the coordinated functioning of individual cells, and finally become involved in the chemical and physical properties of protoplasm.

The parts that are involved and the way in which they are organized differ widely from one type of organism to another; but in any terrestrial animal large enough to see and handle, we shall find that there are a high degree of differentiation of parts and much division of labor; that the individual comprises a number of closely interrelated structural and functional systems; that each system is composed of diverse but coordinated organs; and that the organs are built of tissues, which, in turn, consist of cells and cell products.

The Organism as a Link in a Sequence of Generations. The second viewpoint from which we shall examine the organism is that of its role as a temporary unit in a sequence of similar individuals. When we inquire into the individual's origin, we find that it was produced by parents (in some cases, by a single parent) very like itself; and we find also that each organism has but a limited individual life and will eventually cease to exist. In spite of this limited life span of the individual, however, the race to which it belongs continues, and the organism is more than an individual; it also functions as a member of its race, a link in a sequence of continuing individuals.

Here we encounter a new group of problems. How is the production of a new individual brought about? To what extent, and by what means are the structures and functions of the parent individual reproduced in the offspring and in the offspring's offspring? Does the organism's role as an individual conflict or correlate or have any relations with its role as a member of its race? The answers to these questions not only are fundamental to an understanding of the world of life, but they are the basis for many important human problems—sex and reproduction, the role of biological inheritance in the maintenance of and change in human populations and society, and the individual man or woman's potential value as a contributor to the next generation.

The Organism as the Product of Evolution. From a third and still broader viewpoint, we shall compare an organism with other forms of life about it. We find that its individual pattern of structure and function and the details of its reproductive behavior differ more or less from theirs. We find not only that the individual is a member of a sequence of generations but that it belongs to a much larger assemblage of closely similar forms that we recognize as a kind or *species*, which in most instances will include many thousands or millions of individuals. We shall find that this species is, in turn, a member of a still larger assemblage of several similar species, termed a *genus;* that *genera* (plural of *genus*) can be grouped into *families*, families into *orders*, orders into *classes*, etc., progressively larger and larger groups having less and less closely similar structures.

Altogether, more than a million different kinds of organisms are known to exist, grouped into two great (animal and plant) kingdoms and subdivisible into phyla, classes, orders, families, and genera. When we seek to account for this tremendous variety in the forms of life and compare their various degrees of likenesses and differences, we are led to the conclusion that there is a common blood kinship among all organisms—that their similarities are due to their descent from a common ancestral stock; that the differences among them are due to the remoteness of such common ancestors in the tremendous expanse of past time. Such a concept is more a program of study than a finished statement of detail, but the more data we gather the more certain seems the conclusion; and we see the organism before us as the end product of a long history of survival and change, and see that much of its structure, its functioning and its reproductive processes bear the impress of former adaptations for existence. This concept applies to man as well as to all other organisms and provides the only rational explanation of many human attributes that are inexplicable on any other grounds.

The Organism as a Unit in a Social-economic Complex. Our fourth viewpoint is concerned with another sort of relationship among organisms. No animal or plant "liveth unto itself"; instead it is a member of a complex society of often diverse kinds of organisms, brought together by more or less common responses to particular intensities of heat, light, moisture, etc., and exhibiting various kinds of interdependencies in the competition for the necessities of existence. Much of this interdependence is based upon the fact that the whole organic world is a huge "energy cycle." Energy from the sun, captured by the photosynthesis of green plants, provides the driving power upon which all forms of life are directly or indirectly dependent. The competition for this energy and its transfer from organism to organism involve a host of reciprocal interactions—finding food, competition for food, avoiding being eaten, and cooperation for mutual aid, as well as numerous less direct relationships.

Regarded from this viewpoint, the organism raises a number of new problems. What role does it play in the economy of nature? How does its existence affect the other members of its society? What other organisms affect its own welfare? These are far from simple questions, and to answer them requires a multitude of difficult and subtle observations and much quantitative data. From such observations and such data come much of man's ability to utilize and conserve the living world for his own needs and purposes. Medicine, agriculture, forestry, and the conservation of fisheries, game, and other wild life are dependent upon our knowledge of these relationships.

These four aspects of the organism—its roles as an individual, as a member of its race, as a product of evolution, and as a unit in a competitive society—form the chief subdivisions of this book; but it must also be emphasized that all are related aspects of the same, and of every, organism; that each individual and the niche that it occupies in the organic world has been shaped by that organism's evolutionary history; and that this evolution, in turn, has been produced by the functioning of the organism's ancestors, members of successive races that lived and competed with other organisms in the world about them.

BIOLOGY AS A SCIENCE: THE SCIENTIFIC METHOD AND ITS LIMITATIONS

It is important to keep in mind that biology, in attempting to answer the various questions confronting it, has adopted the methods and technique of a science. Any science is a body of knowledge concerning some particular "field," or group of phenomena, in the universe in which we live. It assumes that the phenomena with which it is concerned are more or less interrelated, and sets out to analyze and precisely describe them and to discover their relationships. Observation and experiment establish facts (*i.e.*, result in agreed-upon descriptions of isolated phenomena); but science is much more than a compilation of such observations. It attempts to summarize and classify its observations and establish relationships among them. Here it utilizes one of its most useful devices, the hypothesis.

A *hypothesis* is a statement that goes beyond the available observations. It postulates a generalization or relationship that is *suggested but not proved* by the facts already known. Its usefulness consists in that it provides an interpretation of available knowledge that can be tested by further observations and experiments. The results of these observations and experiments decide the fate of the hypothesis:

1. It may be found to be untenable, an incorrect summary or assumption.
2. It may be found to be partially tenable, in need of modification and then of further tests.
3. It may prove to be very difficult of direct test, and either be gradually substantiated by indirect evidence or be abandoned for other and more fruitful hypotheses; or it may long retain its status as an unproved but useful concept.
4. It may be clearly demonstrated or shown to be so highly probable that it ceases to be regarded as a hypothesis and then becomes one of the accepted *principles* or "laws" of the science.

Any science consists, then, of a mass of "facts" derived from observation and experiment; and of summations, classifications and interpretations of these facts that are in part regarded as proved (principles, "laws") and in part are hypotheses in various stages of acceptance or rejection.

One of the main requisites of science and the scientific method is the objective viewpoint. This is the ideal and, largely, the practice of making all observations and all proposals and tests of hypotheses without any personal bias. It holds that how gratifying or how abhorrent an observation or a hypothesis may seem has no possible bearing on the scientific truth or falsity of that observation or hypothesis; that *the testimony of checked and repeated observation and experiment is the final authority on which truth or falsity must rest.*

The gathering of precise observations, the free use of hypotheses, and the objective viewpoint are all characteristics of the scientific method; but their fruitful use depends upon the desire to know, a constructive imagination that "sees" relationships between formerly isolated observations, and a degree of critical skepticism that scrutinizes the accuracy of observations and the validity of the conclusions drawn from them.

It is also important to keep in mind that science and the scientific method have limitations. From its very nature science is man-made; it has rejected any thought or expectation of a Mount Sinai, whence absolute truth can be received with final authority. Such authority as it has is due to the consensus of its accepted practitioners and to the fact that it provides the most accurate account of its phenomena that man has yet discovered. Moreover, from a practical standpoint, it is often difficult to know where fact and proved principle leave off and hypothesis begins. Indeed, scientific facts are often partial and incom-

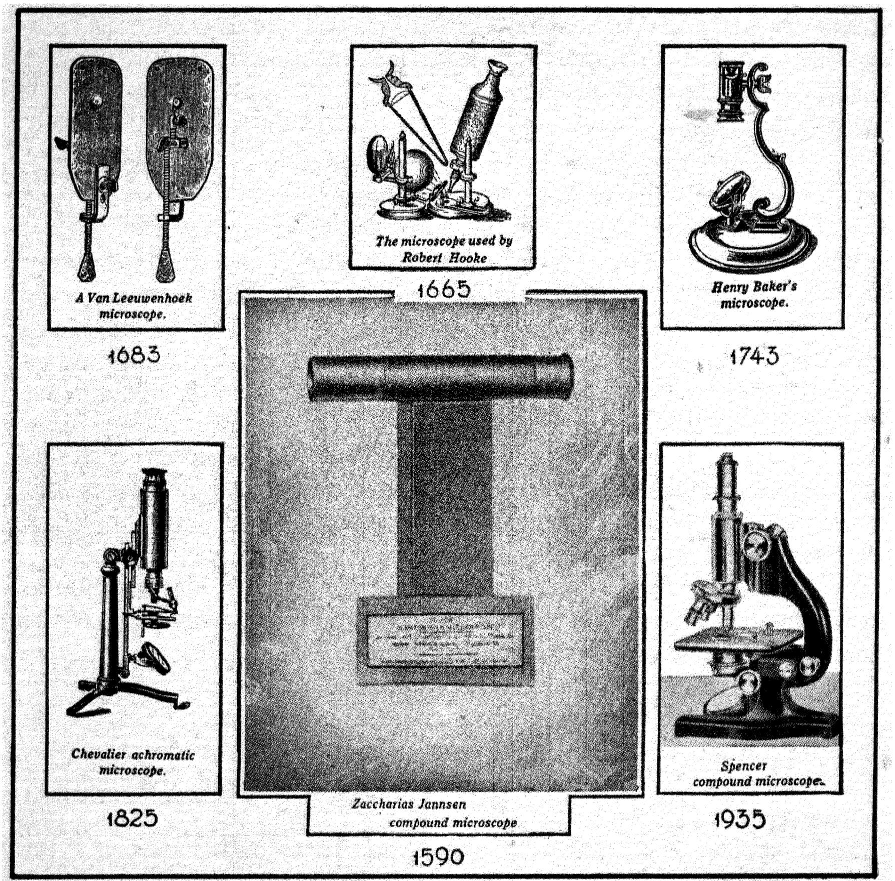
A Van Leeuwenhoek microscope.
1683
The microscope used by Robert Hooke
1665
Henry Baker's microscope.
1743
Chevalier achromatic microscope.
1825
Zaccharias Jannsen compound microscope
1590
Spencer compound microscope.
1935

FIG. 1. *Some microscopes from the sixteenth to the twentieth century. (From "The Laboratory," Fisher Scientific Company and The Spencer Lens Company.)*

plete, selected and understood because they appeared to answer the question in mind at the time they were selected and verified. Further, as was stated in a preceding paragraph, science *assumes* that the phenomena with which it deals are related and that there is a definite orderliness in nature. This assumption lies back of all science and in a strict sense is probably incapable of proof, and even if this assumption can be accepted as true, science can hope only to answer questions of "how," not questions of "why" unless we are to define "why" in terms of "how." Finally, as Sir Francis Bacon pointed out 400 years ago, we must "ask nature fair questions." Many questions that we propose unwittingly take for granted conditions that do not exist. For example, the old question of "how (or why) does the seeing of a rabbit by a pregnant woman cause a hare-lip in her child" is "unfair," because it has assumed an unproved affirmative answer to an unrecognized antecedent question, "Does seeing a rabbit cause a hare-lip in the child?"

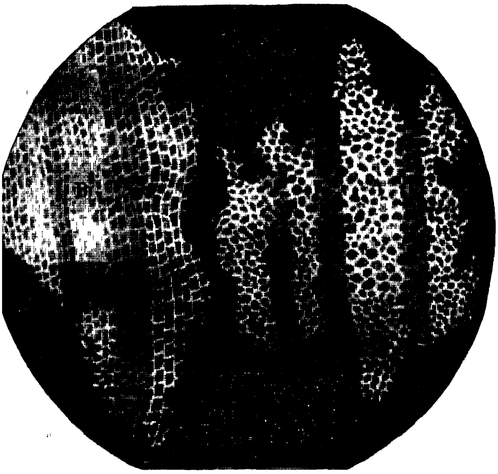

FIG. 2. *Robert Hooke's illustration of the cells in cork, from his "Micrographia," published in 1665.*

The Development of the "Cell Doctrine" as an Example of the Growth of a Hypothesis into a Principle. Since we are soon to be concerned with cells and their roles in the structure, functioning, development, and inheritance of the organism, the gradual development of the modern cell doctrine, or cell principle, forms a pertinent example of the steps by which an accumulation of facts may lead to a hypothesis and the hypothesis become established as an accepted principle.

1. *The accumulation of observations* began soon after the discovery of the microscope and was doubtless long retarded by the slow development

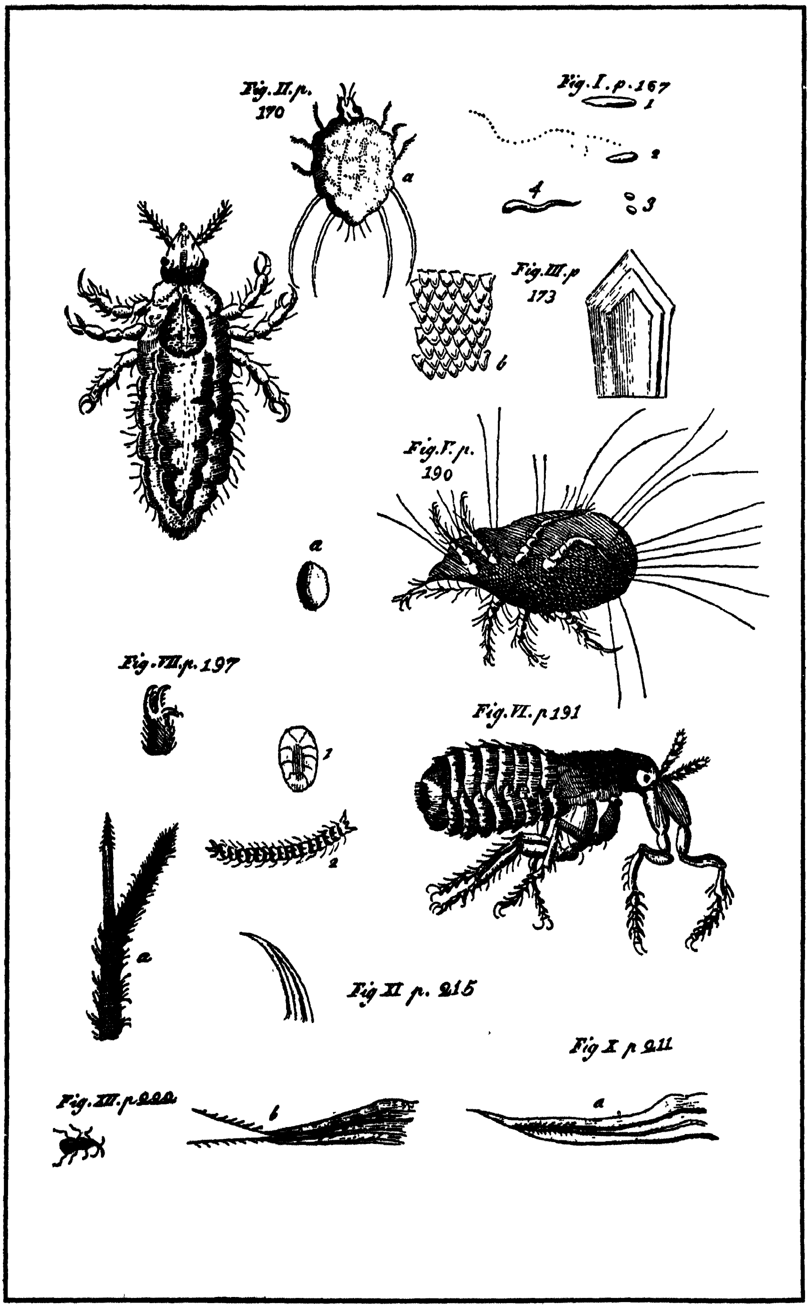
Fig. II. p. 170
a
Fig. I. p. 167
1
2
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3
Fig. III. p 173
b
Fig. V. p. 190
a
Fig. VII. p. 197
1
2
a
Fig. VI. p 191
Fig XI p. 215
Fig X p 211
Fig. XII. p. 222
b
a

Fig. 3. *Sketches of objects seen through the microscope of Henry Baker—1743. (Courtesy of The Spencer Lens Company.)*

of satisfactory microscopes. Robert Hooke (1635–1703) first observed cellular structure in cork and other plant tissues, and named the small spaces he saw *cells.* Malpighi (1628–1694), in Italy, in making microscopic studies of insects, plants, and the tissues of man, remarked on the "repeated vesicles" that appeared to make up many of the tissues he examined. Other students of plant and animal structures from time to time saw and mentioned that various parts of their specimens were composed of microscopic units that they called by various names and interpreted in various fashions. By the early part of the nineteenth century, these observations became more frequent and included many kinds and parts of plants and a smaller number of animal tissues; however, no great interest or importance was attached to these findings.

2. *The Statement of a Hypothesis.* In 1839, two men, the botanist Schleiden and the zoologist Schwann, announced the hypothesis that "all living things are made of cells." They came to this conclusion partly from the work of others and partly from their own investigations, which had been particularly directed toward an examination of a large number of plant and animal parts in a search for cellular structure. Note that their statement went far beyond any possible actual observations that Schleiden and Schwann could have made or gathered from the writings of others. Only a small fraction of the multitude of living things had been examined for cells, and not all parts of any one organism had been thoroughly explored, but wherever Schleiden and Schwann had made a careful microscopic examination they had found cells, and they had also noted that cellular structure is often hard to detect and is to be demonstrated only by careful methods of investigation. Both Schleiden and Schwann had many erroneous ideas about cells. They regarded them as empty sacs or spaces enclosed by walls and believed that cells were formed from noncellular materials, much as crystals are formed in solutions.

3. *Corrections, Modifications, and Extensions of the Original Hypothesis.* The published hypothesis of Schleiden and Schwann at once stressed the importance of cells and attracted the attention of many other microscopists. New observations were made, more materials were examined, and the structure of the cell itself was scrutinized. It was found that some tissues—bone and cartilage, for instance—are built not of cells but very largely of substances that bone-forming and cartilage-forming cells produce. The cell was found not always to have a wall but to consist more essentially of a peculiar stuff called *protoplasm.* It was also found that cells do not crystallize out of noncellular stuff but instead are invariably formed by the division of a previously existing cell.

4. *Establishment of the Corrected Hypothesis.* Within another 20 years, as the result of the observations and experiments of a large group

of talented workers, the cell theory was restated somewhat as follows: all living things are composed of cells or of cells and cell products; the cell consists of a bit of protoplasm containing a nucleus; and cells are always derived from other previously existing cells. This statement still stands today and is now accepted as entirely substantiated. We no longer speak of the cell hypothesis but of the cell doctrine or cell principle.

PART I

THE INDIVIDUAL ORGANISM

CHAPTER II

The Organization of the Individual

Our own bodies furnish an excellent example from which to study the structure and functioning of the individual. Although man is among the most complex of all organisms, he is built upon the same basic plan as any other familiar animal, and from the standpoint of a functioning biological machine, he is little, if any, more difficult to comprehend than would be a cat, a frog, a fish, or even a spider or a crayfish.

When we attempt to understand the structure and functioning of any of these animals, we encounter the high development of organization from which our overworked term *organism* is derived. This organization is roughly comparable to that of some huge, modern factory. In an automobile factory, for example, each worker or group of workers specializes on some one detail. The work performed by any one individual or group is meaningless in itself, but the cooperation of some groups results in the production of an engine, that of other groups in a chassis, of still others in a body; and finally, when still other specialists assemble engines, chassis, and bodies into automobiles, we see that the highly organized specialization of workers, departments, and divisions forms a complete and efficient whole.

In the human (or any higher animal) body, specialization, division of labor, and coordination are far more detailed and intricate than are found in any factory, but, just as in the factory, differentiation of parts and division of labor are so organized and coordinated as to result in a whole—in this case, in a single individual organism. Fortunately for our ease of comprehension, the several divisions, departments, and subdivisions of the animal body, however greatly they differ in detail, can be classified into a relatively few types of organizational groups. This general plan of the organization of the higher animals is given below.

SCHEME OF ORGANIZATION OF THE HUMAN BODY

1. The *living body* is a self-maintaining unit or individual composed of a number of closely integrated systems.

2. *Systems* are major physiological or functioning divisions of the body, each concerned with the performance of some closely related group or sequence of body functions. The digestive, locomotor, circulatory, nervous, and excretory systems are good examples, and each of these can be subdivided into a number of connected and coordinated organs.

3. *Organs*, as major subdivisions of a system, accomplish some essential and more or less complex tasks in the total functioning of the entire system. To illustrate, the stomach is one of the organs that make up the digestive system, in which it plays certain essential but incomplete parts in the whole digestive process. Organs, in turn, are composed of a number of appropriate and coordinate tissues.

4. *Tissues* are groups of similar cells (or of cells and their common products) united to fulfill a common function. The stomach, for example, is made up of muscular, secreting, connective and other tissues that in combination make possible the complex functions performed by that organ. Each tissue is found to consist of a group of similar cells or of cells and their common product.

5. *Cells.* Here we have reached, not the ultimate parts of the body, but a very real *biological unit* of structure and functioning, in that the cell is not divisible into any smaller living units. The human body comprises billions of individual cells that show hundreds of kinds of structural and functional specializations; but all are alike in certain fundamental structures and properties, and all are composed chiefly of the peculiar living stuff we know as protoplasm.

SOME STRUCTURES AND PROPERTIES OF PROTOPLASM

A complete definition of protoplasm is not possible from our present-day knowledge. We know that it is the living stuff; that it is extremely complicated; and that it is not a chemical compound but rather a physical system in which many, and often highly complex, chemical substances are mingled in intricate relationship. Chief among the chemical substances that are essential and invariable constituents of protoplasm are a number of highly complex compounds called *proteins.* These are characterized by containing nitrogen, as well as oxygen, hydrogen, and carbon, and always contain one or more of the amino acids. Other chemical compounds essential to protoplasm are various fats (in the form of oil droplets), carbohydrates, a number of mineral salts, and water.

Physically, protoplasm exhibits what is known as a *colloid* condition. This means that it consists of a fluid or semifluid substance in which a tremendous number of exceedingly minute (probably spherical) particles are suspended; the particles are separated from one another by the fluid or semifluid that contains them. In the simplest colloids known (and these have extremely complicated properties), only two substances are present, the *continuous* surrounding substance and the finely divided (usually submicroscopic) *discontinuous* particles suspended in the continuous substance. In protoplasm, the continuous substance is apparently a complicated watery solution, in which a large number of different kinds and different sizes of discontinuous particles occur. There is even evidence that some of the larger particles are themselves, in turn, minute colloidal systems. The total amount of surface provided by the tremendous number of discontinuous particles is very large, and these surfaces are the region of many complicated electric and other physical phenomena that are as yet but imperfectly understood. Further, adding to the complexity of its study, protoplasm is constantly changing; not only are chemical and physical changes going on within it but new substances are being taken in from outside and other substances are being thrown off. Although we cannot define protoplasm, we have come to recognize many of its inherent and invariable properties.

Nonvital Properties. Many of the properties exhibited by protoplasm are not peculiar to it but are exhibited also by various nonliving systems. These nonvital properties are nevertheless very important in explaining many of the activities and functions of protoplasm and the cell. Among the nonvital properties of protoplasm are *diffusion* and *osmosis;* various surface phenomena such as *surface tension* and *adsorption;* and a host of chemical relationships and reactions.

Vital Properties. Protoplasm shows a number of other properties that are not so clearly exhibited by nonliving systems. These may be due to some peculiar vital principle of protoplasm, or they may be (and more probably are) merely too complicated to be understood in terms of present-day physical and chemical knowledge.

1. *Metabolism.* All protoplasm (unless temporarily dormant) is constantly capturing energy and utilizing it for activity or growth. (Storage of energy and its subsequent use may add another step to the process.) This property, particularly the ability to change energy (food) into more protoplasm (*i.e.*, growth), appears to be peculiar to protoplasm.

2. *Reproduction.* All units of protoplasm have the power to divide and produce new units of the same kind. This is in part dependent upon growth but also involves the maintenance of a constant type and size of organization in spite of growth.

3. *Irritability or Reactiveness.* This is the property of responding to stimuli. A large number of both external and internal stimuli—light, temperature change, contact, gravity, electric current, change in degree of acidity or alkalinity, and various chemical substances—cause more or less appropriate responses on the part of protoplasm.

THE STRUCTURE OF THE CELL

The simplest description of a cell would be "a small mass of protoplasm differentiated into nucleus and cytoplasm." The size of this "mass of protoplasm" varies widely among different kinds of cells, but the great majority of cells are microscopic, not at all visible to the unaided eye. Some few cells, chiefly egg cells that are enlarged by stored food, are so large as to be easily visible; some muscle cells have lengths that are measured in inches; some nerve cells, lengths that are measured in feet; but these elongated cells are extremely slender. On the other hand, a large number of cells require rather high magnifications (100 times or more) to be visible at all. Cells vary widely in shape (Fig. 6), although all cells of one kind have a similar shape as well as a similar size.

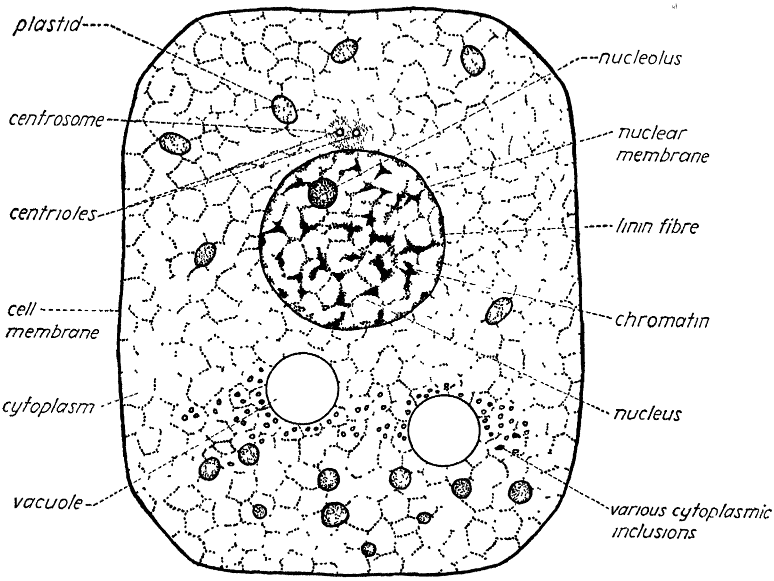

FIG. 4. *A diagram of a typical cell illustrating common structures found in plant and animal cells. (Courtesy of the General Biological Supply Company.)*

When we examine a cell beneath a microscope (Fig. 4), we find that both the nucleus and the cytoplasm have characteristic structures. In many instances, these will require a special treatment (staining) and careful manipulation of the microscope in order to be seen.

The Structure of the Nucleus. The nucleus is usually, but not always, centrally located in the larger mass of cytoplasm and separated from the latter by a thin *nuclear membrane.* This nuclear membrane is usually turgid from the contained *nuclear sap,* a clear fluid that fills all parts of the nucleus not occupied by other structures. Barely visible within this space is a loose, irregular network of fine *linin* fibers. Scattered about among the fibers are some strongly staining, variously shaped particles of a substance called *chromatin*. This material is really the most important part of the nucleus, and it is not improbable that all the rest of the nuclear structures are entirely supplementary to it. At one spot, just outside the nucleus, is a small body, the *centrosome,* that contains one or two granules, the *centrioles*. Although they are outside the nuclear membrane, the centrosome and centrioles function as a part of the nucleus. In addition to the structures just mentioned, many nuclei contain a strongly staining body, usually larger than any of the chromatin particles, called a *nucleolus*.

The function of the nucleus appears to be largely regulatory. It is definitely essential to the continued life of a cell, although cytoplasm that has been deprived of its nucleus may continue to live for a time. Later, we shall be especially concerned with the behavior and some of the important functions of this chromatin material.

The Cytoplasm. All the protoplasm outside the nucleus is termed *cytoplasm,* and it, too, is divided into various parts and regions. In all cells, the outermost part of the cytoplasm is differentiated into an exceedingly thin cell membrane. Between the cell membrane and the nucleus, the cytoplasm is frequently divided into two general regions—the peripheral *ectoplasm* and the inner *endoplasm*—that have somewhat different optical properties. Other structures frequently found in the cytoplasm and often characteristic of certain kinds of cells are *vacuoles*—small, usually spherical spaces containing fluids of various sorts; and *plastids*—more or less solid, often disk-shaped bodies that contain specialized parts of the living cytoplasm and have various special duties to perform. The cytoplasm may also contain nonliving inclusions (often in the form of granules), such as stored food, cell products, and wastes. Finally, around many cells (nearly all plant and some animal cells) is found a *cell wall*—a nonliving product of the cytoplasm and a structure that is often regarded as one of the cell parts.

CELL DIVISION

The foregoing description of a cell applies to the so-called "resting stage," when the cell is carrying on its various metabolic processes and is only resting in the sense that it is not dividing. Since, however, the only way in which any cell is ever known to come into existence is through the division of a parent cell and since, in division, it goes through a series of changes that give much information about its various parts, any discussion of the cell must provide some account of its normal process of division. Actually, the process appears to be more or less continuous and unbroken from its beginning until two separate daughter cells are formed, but it is convenient and customary to recognize four successive stages in this process. The account that follows will be much more readily understood if frequent comparisons are made to the rather diagrammatic drawings of Fig. 5.

The *prophase* extends from the end of a resting stage to the actual splitting of the chromosomes. At the beginning of the prophase, the apparently scattered particles of chromatin[1] begin to form a number of elongated, thin threads, the *spireme;* and the centrosomes begin to separate, with the gradual appearance of faint, raylike lines about them and of fine spindle fibers that connect them. Gradually the threads of the spireme become shorter and thicker and come to be located in the vicinity of the equatorial plate of the nucleus. At this time it can be seen that the chromatin of the nucleus consists of a number of (usually) rodlike structures called *chromosomes;* and if a number of late-prophase nuclei from the same species of organism are compared, it will be seen that the chromosomes in each cell are identical in number and in shape with those in all other cells. In the meanwhile, the two centrosomes have moved 180 degrees apart and now occupy opposite poles of the nucleus, and the nuclear membrane has disappeared so that there is no visible boundary between the cytoplasm and the nuclear structures. Between the two centrioles there now extends a spindle-shaped figure of fine fibers, its two apices ending in the centrioles, and its expanded central portion in the equatorial plate of the nucleus. Thus, by the end of the prophase, the chromatin has been formed into a definite number of chromosomes that lie in or near the equatorial plate of the nucleus, the nuclear membrane has disappeared, and the two centrioles, on opposite sides of the equatorial plate, mark the apices of two spindle-fiber cones, the bases of which meet in the equatorial plate.

In the next stage, the *metaphase,* each of the chromosomes splits longitudinally into exactly equal halves.

In the third stage, the *anaphase,* the halves of each chromosome begin to move apart toward the centrioles. Spindle fibers from each centriole are apparently attached to the half chromosomes on their side of the equatorial plate and, by shortening, gradually draw the two sets of half chromosomes apart and toward the poles of the former nucleus. By the end of the anaphase, the two sets of half chromosomes are approximately the width of the old nucleus apart.

In the last stage, the *telophase,* the spindle fibers largely disappear, a new nuclear membrane forms about each mass of chromatin, each centriole divides, and the cytoplasm is divided by the formation of cell membranes that cut the old cytoplasmic mass into two complete new cells. From the telophase, the new daughter cells pass into the resting stage, during which their cytoplasm and chromosomes grow again to full size.

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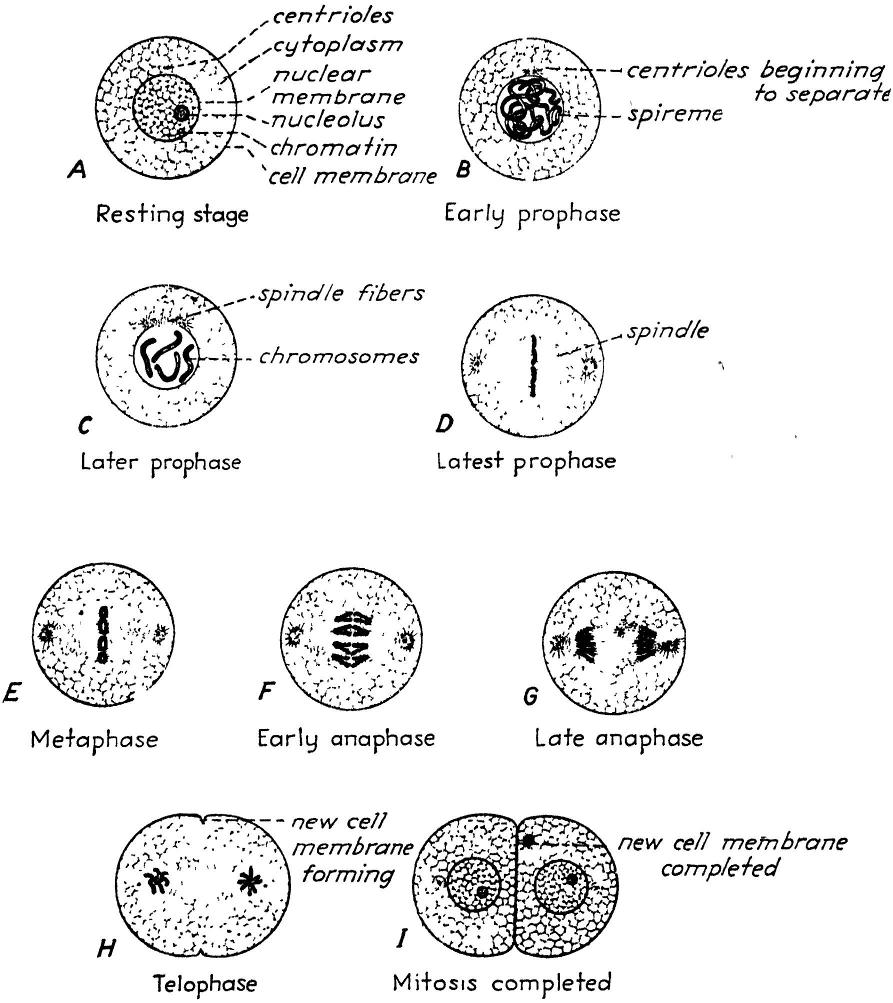
[1] There is very strong evidence from several sources that these particles are actually, although invisibly, held together throughout the resting stage as parts of their respective chromosomes.


centrioles
cytoplasm
nuclear membrane
nucleolus
chromatin
cell membrane
A
centrioles beginning to separate
spireme
B
spindle fibers
chromosomes
C
spindle
D
E
F
G
new cell membrane forming
H
new cell membrane completed
I

Resting stage

Early prophase

Later prophase

Latest prophase

Metaphase

Early anaphase

Late anaphase

Telophase

Mitosis completed

FIG. 5.—*Diagrammatic representation of successive stages in mitosis, the typical process of cell division in animals and plants.* (*Courtesy of the General Biological Supply Company.*)

This, the normal method of cell division, is termed *mitosis* (Greek, *nitos,* "a thread"), in reference to the conspicuous, threadlike spireme. Mitosis results in a *quantitatively and qualitatively equal division of the hromatin* at each cell division.

Mitosis in plant cells is very similar to that described above except that in most plant cells no centrosomes are found, and, since a cell wall is generally present in addition to the cell membrane, the cytoplasmic division in the telophase is marked by the development of a cell-wall plate between the two daughter cells.

TISSUES AND GLANDS

A tissue may be either a group of like cells, so connected as to perform a common function, or the common product of a group of similar cells. In any of the higher animals, scores of different kinds of tissues may be recognized, but for our purposes we can group all tissues into four great groups.

1. *Sustentative tissues* are adapted to provide mechanical support and to bind various other tissues together. In addition, certain types of sustentative tissues are modified for such special functions as fat storage or the formation of a circulating medium. Examples of sustentative tissues are bone, cartilage, ligament, tendon, and the cells and fluids of the blood. Many of these tissues are chiefly cell products, their living cells functioning to provide the needed material rather than to perform the necessary tasks directly.
2. *Contractile tissues* include various types of muscle cells; all are adapted to perform work by contracting or shortening.
3. *Nervous tissues* are specialized to receive and transmit stimulations.
4. *Epithelial tissues* are variously specialized to cover the external and internal surfaces of the body. The formation of glands is a characteristic and peculiar property of epithelial tissues.

Glands are cells or groups of cells that have the function of *secreting* some substance needed in the economy of the body or of *excreting* some waste product or surplus substance. In all glands, the actual secreting (or excreting) cells are derived from epithelial tissues, although these may be supplemented by various sustentative and contractile tissues. In some instances, single epithelial cells (gland cells) function as glands, but typically glands are aggregations of a number of secreting (or excreting) cells that are able to produce a comparatively large quantity of their particular product.

Ordinarily, we think of a gland as being connected with some epithelial surface (the skin or the lining of the gut) by a passageway or duct, through which its products may pass. Examples of such glands will be found in the skin and in the digestive glands of the mouth, stomach, and intestine. Another very different kind of gland will be considered when we come to study the endocrine system.

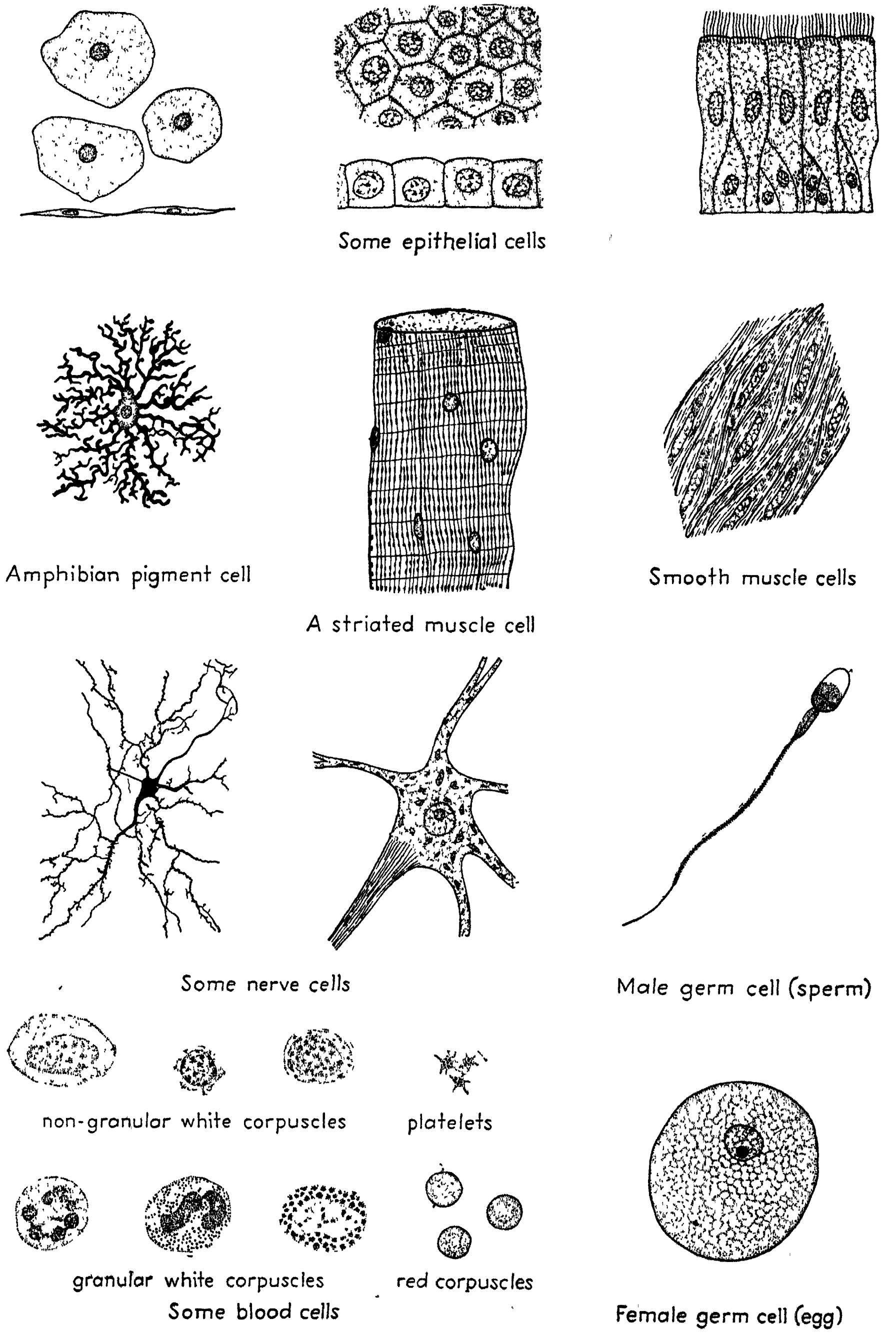

Some epithelial cells
Amphibian pigment cell
A striated muscle cell
Smooth muscle cells
Some nerve cells
Male germ cell (sperm)
non-granular white corpuscles
platelets
granular white corpuscles
red corpuscles
Some blood cells
Female germ cell (egg)

FIG. 6. *Types of animal cells illustrating cell differentiation and division of labor.* (*Courtesy of the General Biological Supply Company.*)

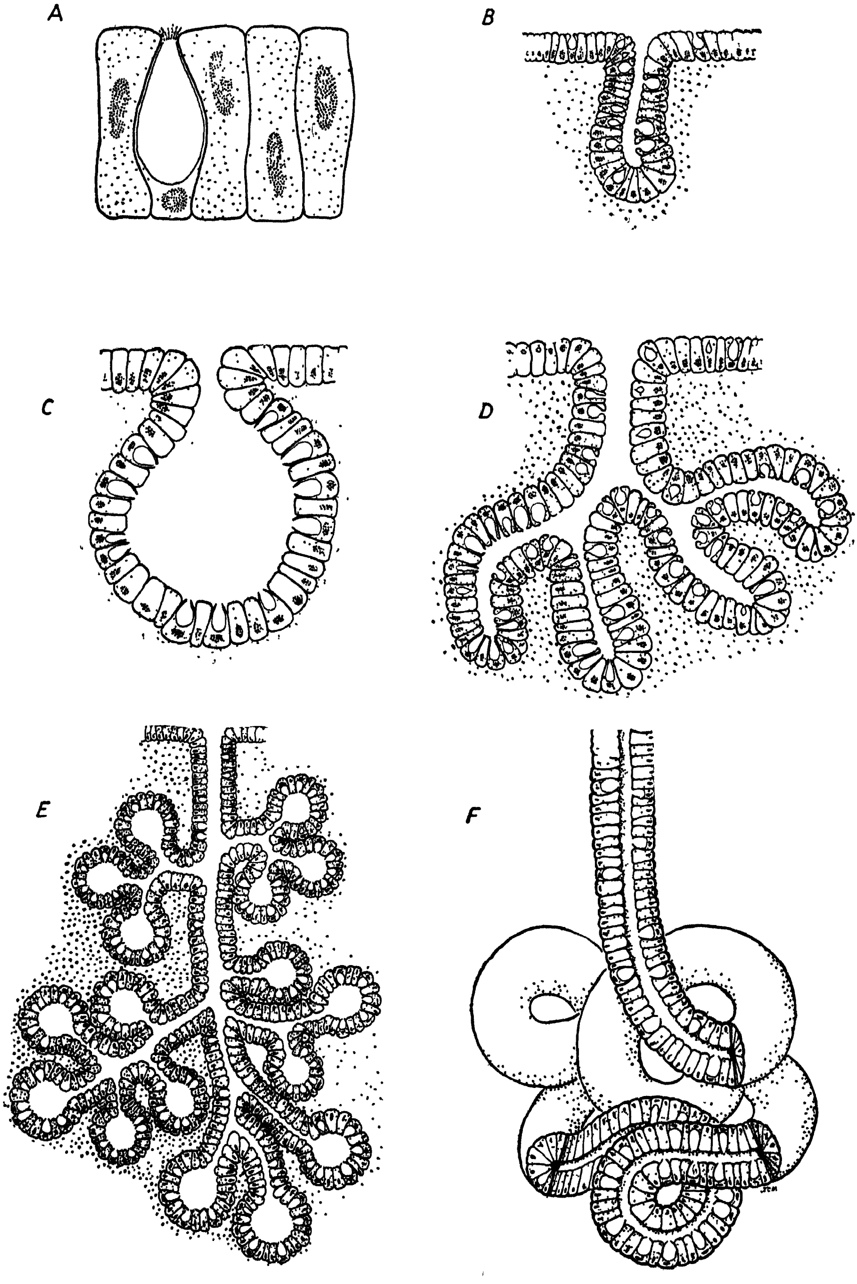


Fig. 7. *Types of glands.* (*A*) *Glandular cells in epithelium;* (*B*) *simple tubular gland* (*C*) *simple alveolar gland;* (*D*) *compound tubular gland;* (*E*) *compound alveolar gland;* (*F*) *simple coiled tubular gland* (*sweat gland*).

ORGANS AND SYSTEMS

Organs and systems represent successively higher stages in body organization. As the term is used here, an organ is typically composed of a number of diverse kinds of tissues brought together to perform some definite and limited function that requires the cooperation of several or many kinds of cells. A skeletal muscle, for instance, is an organ to perform motion, and requires not only a mass of voluntary muscle tissue but also sustentative tissues to hold the muscle tissues in proper arrangement and protect them from friction. Other sustentative tissues connect the muscle bundles with the skeleton; blood and blood vessels supply materials for energy and remove wastes; and nervous tissues help coordinate these other parts and control the muscle's action. But a single muscle is rarely capable of performing any useful action. Even the simplest voluntary movements necessitate sets of muscles, skeletal supports and joints; and when we attempt to understand even the mechanics of our voluntary movements, we find that hundreds of different muscles are precisely attached to definite parts of a bony framework to produce a motor or locomotor system composed of many precisely coordinated organs.

Other examples of organs and systems are the eyes, ears, nose, and many other "sense organs" that, together with the brain, the spinal cord, and other parts, form the nervous system; or the mouth, esophagus, stomach, intestines, etc., that are united and coordinated into a digestive system.

The Integrating Physiological Systems of the Human Body. Just how many and what systems are to be recognized in the human body is to some extent a matter of how we choose to subdivide and classify and, perhaps, of whether we are more influenced by structural or functional considerations. The usual number recognized varies from 8 to 10, and we shall compromise on 9. These are:

1. The *locomotor system,* which supplies protection and support for other body parts and provides for motion, locomotion, and heat production. Often listed separately as the *skeletal* and the *muscular* systems.
2. The *skin* or *integumentary system,* adapted to perform a number of rather diverse functions that are related and correlated by the necessity of their location at the body surface:
   a. Protection of the body against water loss, light, mechanical injury, and the attack of parasitic organisms.
   b. Heat regulation—a function performed in cooperation with the circulatory and nervous systems—a thermostatically controlled radiator.

   c. Sensory perception—the skin is the location and support of a multitude of varied sense receptors for touch, temperature, etc.
3. The *digestive system,* which has for its function the ingestion of foods; their processing into absorbable component parts; and the delivery of these end products to the circulatory system.
4. The *respiratory system,* which has for its function the providing of an adequate gaseous exchange between the blood and the outside air.

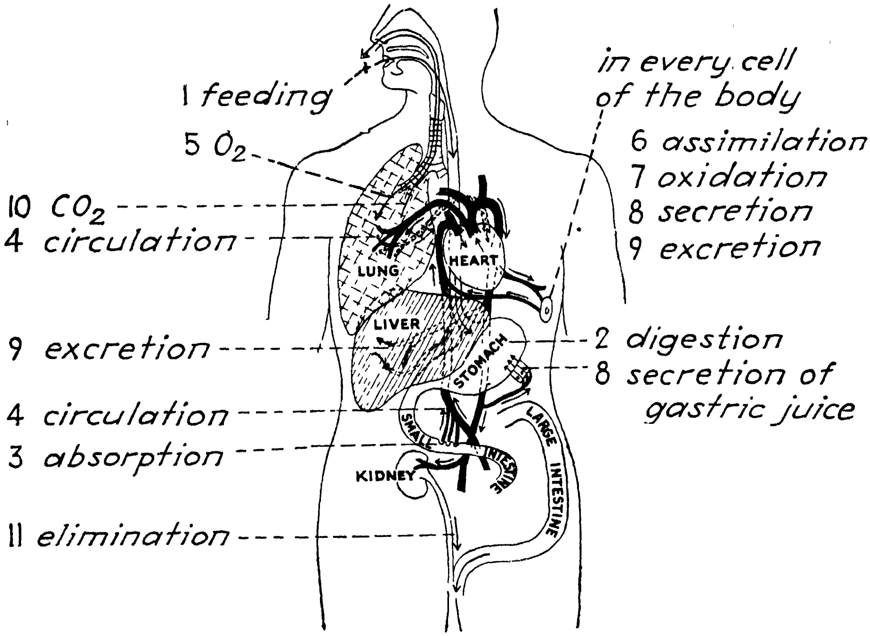

1 feeding
5 O_2
10 CO_2
4 circulation
9 excretion
4 circulation
3 absorption
11 elimination
in every cell of the body
6 assimilation
7 oxidation
8 secretion
9 excretion
2 digestion
8 secretion of gastric juice
LUNG
HEART
LIVER
STOMACH
SMALL INTESTINE
LARGE INTESTINE
KIDNEY

FIG. 8. *Some of the physiological processes associated with various organs and systems of the human body, indicated diagrammatically.* (*From Wolcott, Animal Biology.*)

5. The *excretory system,* which has as its function the elimination of an important part of the wastes that are invariably produced by the living process. Structurally related to item 9 below and sometimes lumped with it as the *urinogenital system.*
6. The *circulatory system,* a common carrier system of pumps, pipe lines, and loading platforms that connects and keeps coordinate the other systems of the body and has accessory but very important functions of protection against invasion by parasitic organisms.
7. The *nervous system,* which receives sensory stimuli from the outside world and from other body regions, and functions as a special coordinating system between the various body parts and between the body and the outside world.

8. The *endocrine system,* a complex of widely separated glands of internal secretion that provide an important accessory control over body coordination.
9. The *reproductive systems,* male and female in separate bodies, the organs containing the reproductive cells (ovaries or testes) and various supplementary organs, structurally combined (especially in the male) with the excretory system, the two frequently grouped together as the *urinogenital system.*

None of these systems is complete in itself. Each is a specialized functional division of a highly integrated single individual. Their segregation is very useful for analysis, but no system can be wholly understood unless it is recognized as but one dependent part of a whole.

CHAPTER III

The Framework of the Body

The form and symmetry of the human body, as well as the greater part of its bulk and weight, are formed by its skeletal framework and the muscles and skin that cover it. It is the combination of skeleton and muscle that performs all the voluntary movements, makes possible locomotion, and, with the skin, forms a protection and support for nearly all of the more delicate internal organs. Moreover, it is the muscles that utilize most of the energy taken into the body, that provide the greater part of the body heat, and that produce most of the waste that must be continuously eliminated.

THE LOCOMOTOR SYSTEM

Because the skeletal system and the skeletal muscles are so intimately related in their functioning, they are frequently considered together under the heading *locomotor system.* A study of the structures involved in a simple movement of the arm (Fig. 18) will illustrate the interdependence between the skeleton and the muscles that surround and cover it.

The Skeleton. Protoplasm, as we have seen, is largely made up of water. It tends to keep a definite volume but cannot keep a definite shape unless it is held in by some membrane or wall. In the instance of single cells and of the smaller and simpler multicellular animals, the presence of cell membranes or cell walls gives sufficient support. The larger and more highly developed many-celled animals, especially those that must live upon land, however, have had to develop a more or less complicated accessory supporting mechanism. In the vertebrates, this mechanism consists of an internal skeleton made up of *bones, ligaments,* and *cartilages.* The skeleton not only helps to support the massive protoplasmic elements that constitute the body proper but also provides leverage for the action of the muscles that move the body. It is imperfectly represented by the usual mounted skeleton or by the bones that remain after the rest of the body has disintegrated. In life, the 200 odd bones of the human skeleton are connected into a single framework by a variety of devices. These include dovetailed connections that lock certain bones immovably together, cartilaginous junctures or plates that provide somewhat flexible unions between bones, and joints that are more or less freely movable.

Skeletal Units. The most conspicuous units of the skeleton are obviously the *bones.* According to their shape, these may be classified

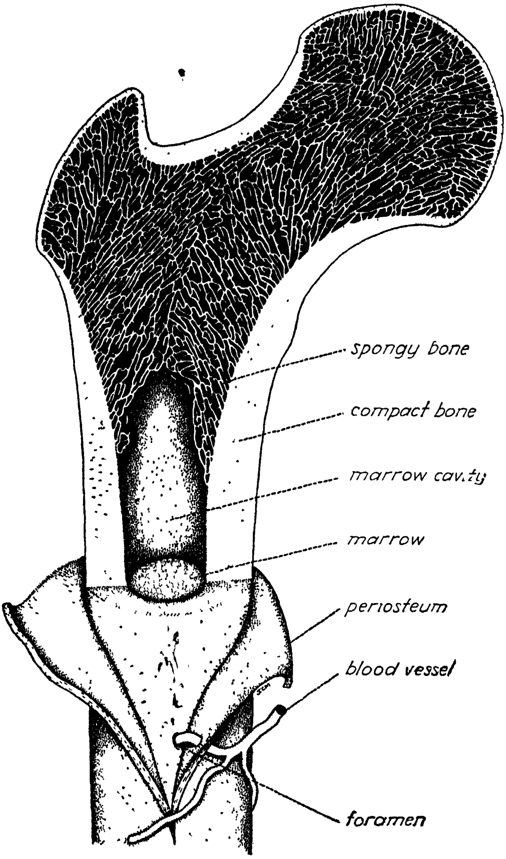


FIG. 9. *A longitudinal section of the head of the femur. Note the structure of compact and spongy bone.* (*Redrawn from Williams, Textbook of Anatomy and Physiology, W. B. Saunders Company.*)

as long bones (*i.e.*, those of the upper and lower arms and legs), short bones (*i.e.*, those of the wrist and ankle), flat bones (*i.e.*, the shoulder blade), and irregular bones (*i.e.*, the vertebrae).

If a long bone is sawed lengthwise and the cut surface is examined, the following parts can easily be identified. There is first a thick, hard outer layer or shell of *compact* bony material; this forms a cylinder surrounding a central cavity, except at the ends, where the interior is filled with a *spongy* open network of bone substance. In life, both the central cavity of the shaft and the meshes of the spongy bone at the ends are filled with a soft tissue called *bone marrow.*

The disposition of the bone substance in the form of a cylinder with internally reinforced ends, instead of a solid rod, gives the bone the greatest mechanical strength attainable for the quantity of structural material used. The strength of the bone is also materially increased by the arrangement of its finer structural elements. The inner and outer walls of the shaft are formed of circumferential layers or *lamellae,* and the spongy bone at the ends of the shaft is not haphazardly arranged but has its partitions aligned in definite planes and curves. A study of these details of structure, in relation to the work done by the bone, shows that they form a pattern giving maximum resistance to the stresses to which the bone is exposed. The same structural efficiency is found in the arrangement of the materials in other bones of the skeleton.

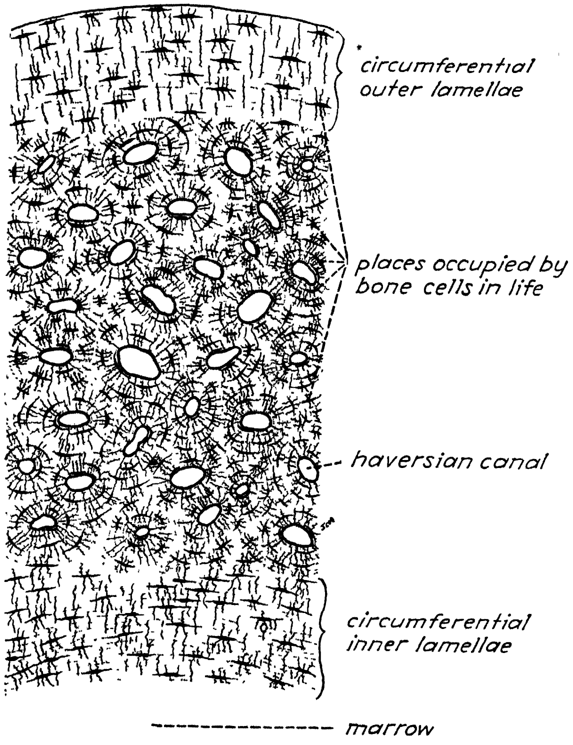

circumferential outer lamellae
places occupied by bone cells in life
haversian canal
circumferential inner lamellae
marrow

FIG. 10. *Cross section of dead bone, taken from the wall of one of the long bones, and extending from the marrow cavity to the outer surface.* (*Redrawn from Williams, Textbook of Anatomy and Physiology, W. B. Saunders Company.*)

All the materials that are utilized in bone, cartilage, and ligament belong to the group called *sustentative tissues* and are notable for being largely composed of cell products rather than cells. In the living body, these products everywhere contain the living cells that produce them. In the case of bone, the cell product is in large part limy salts and persists long after death in the familiar dried bones of a skeletal preparation. In the ligaments, the cell products are elongated, very strong fibers, some elastic, others nonelastic; in cartilage, the cell product is a tough, usually transparent material that, beneath the microscope, is seen everywhere to enclose the cartilage-producing cells. In bone, the matrix consists both of calcium phosphate, which makes the bone hard, and of a strong and tough organic material that pervades the mineral parts. One can take two fresh bones from a recently living body, burn one to remove the organic parts, and place the other in acid to remove all minerals. In the first case, he obtains a dry, brittle "bone"; in the other, a tough, organic, but now flexible structure that still preserves the recognizable shape and dimensions of the original bone. Figures 10 and 11 show, at least diagrammatically, the relationship of the *matrix*, or cell product—in cartilage and bone—to the cells that produce it. In addition, the matrix is penetrated by nerves and blood vessels that supply the living cells; in bone, these occupy the Haversian canals.

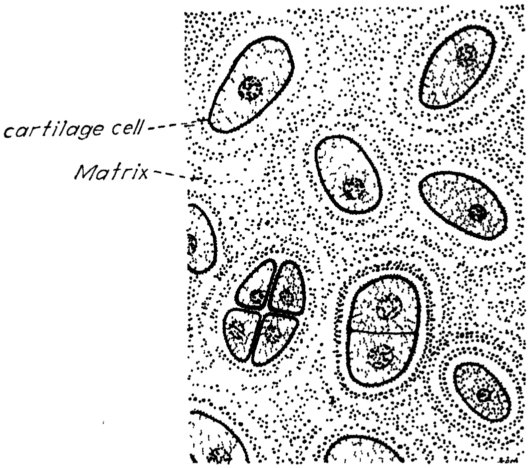


FIG. 11. *Cross section of cartilage.*

The Divisions of the Skeleton. The complete human skeleton is shown in Fig. 12. Two chief regions of the skeleton may be recognized, each with minor subdivisions. The *axial skeleton* comprises the head and backbone (skull and vertebral column), together with the ribs, the sternum, and the cartilages that connect the front or ventral ends of the

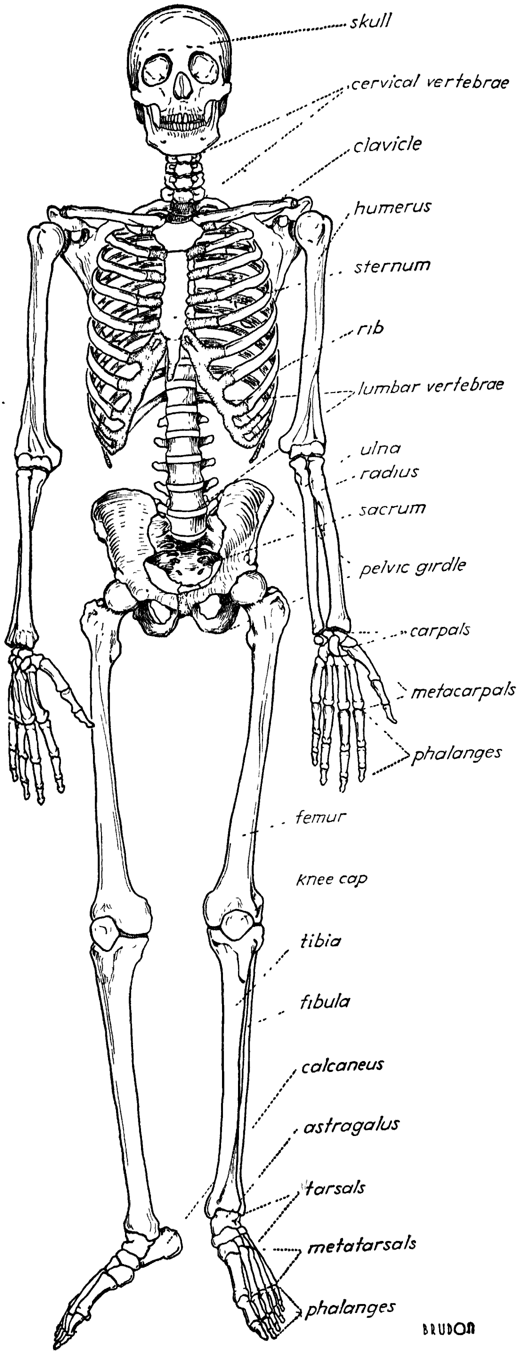

skull
cervical vertebrae
clavicle
humerus
sternum
rib
lumbar vertebrae
ulna
radius
sacrum
pelvic girdle
carpals
metacarpals
phalanges
femur
knee cap
tibia
fibula
calcaneus
astragalus
tarsals
metatarsals
phalanges
BRUDON

FIG. 12. *The human skeleton.*

ribs. In addition, the skeleton includes two so-called "girdles" and their appendages—an upper one, the shoulder or *pectoral girdle,* to which the arms are attached, and a lower one, the hip or *pelvic girdle,* bearing the legs. These two girdles and their appendages make up the *appendicular skeleton.*

The Axial Skeleton. The axial skeleton forms the longitudinal or vertical axis of the body. The skull consists of two main parts, the cranium or brain case and the bones of the face. The former is a rigid bony box, averaging between 1,200 and 1,500 cc. in capacity, which, in life, is completely filled by the brain, its membranes, and the thin layer of fluid that insulates the brain from direct attachment to or contact with the bony walls. The bones of the face surround the mouth and nasal openings, form the lower parts of the eye sockets and the bony partition between the nose and mouth cavities. Except for the strongly hinged lower jaw and three pairs of tiny ear bones, all the bones of the skull are immovable and are fused into a single rigid structure by strong, dovetailed sutures between the various bones.

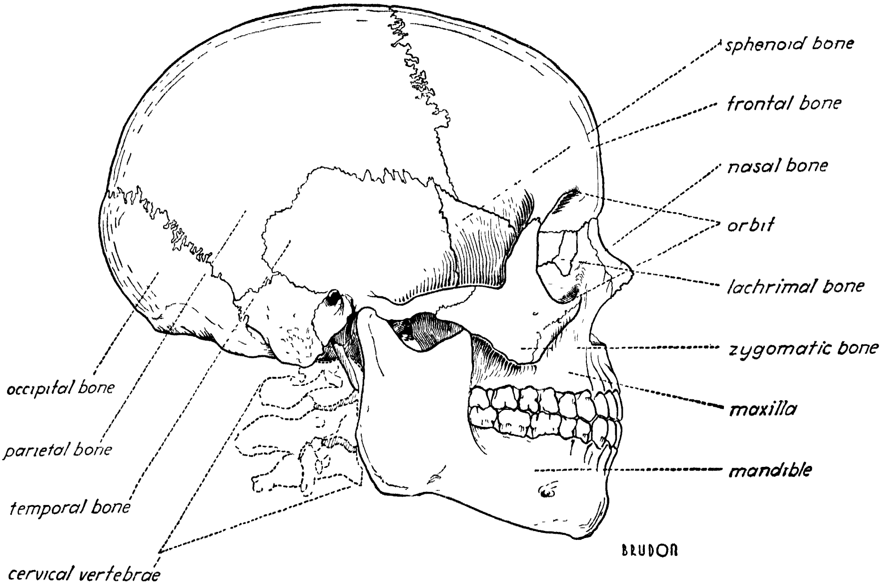


FIG. 13. *The human skull in side view.*

Altogether, the skull comprises some 22 bones, of which 8 pertain to the cranium and 14 to the facial portion. Sixteen lower teeth are borne by the *mandible,* or lower jaw, and 8 by each of the paired *maxillae* that form the upper jaw. The teeth are discussed on pages 49 to 51.

The vertebral column is joined to the skull by a peculiar hinge joint, in which two rounded projections (*occipital condyles*) on the base of the skull fit into corresponding depressions in the uppermost vertebra and permit a limited rocking motion between the two. This provides the up-and-down nodding motion that we can make with our heads; the comparatively limited rotary motion, used in turning the head to either side, is provided by a pivot joint between the first vertebra and the second. Both these motions are limited and restrained by strong ligaments as well as by the muscles of the neck, and so protect the delicate spinal cord (which extends through an opening in the base of the skull into the neural canal of the vertebral column) from being twisted or pinched.

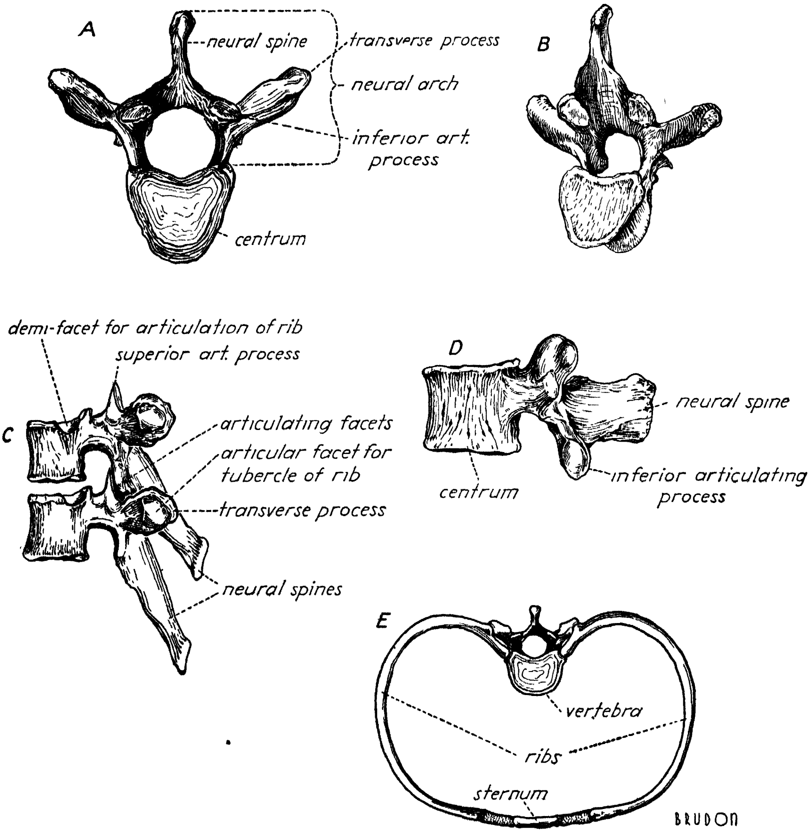

A
neural spine
transverse process
neural arch
inferior art. process
centrum
B
demi-facet for articulation of rib
superior art. process
C
articulating facets
articular facet for tubercle of rib
transverse process
neural spines
D
neural spine
centrum
inferior articulating process
E
vertebra
ribs
sternum
BRUDON

FIG. 14. *Details of the axial skeleton—vertebrae and ribs. (A) Fourth thoracic vertebra, bottom view; (B) fourth thoracic vertebra, lateral view; (C) second and third thoracic vertebra, showing method of articulation; (D) third lumbar vertebra; (E) a thoracic vertebra and attached ribs, the dotted portion joining the ribs to the sternum in front is cartilage.*

The whole vertebral column consists of some 33 bones or vertebrae that are arranged in a linear series from the skull to slightly below the pelvic girdle. All the *vertebrae* are built upon the same general plan but are variously modified in different parts of the column. The large, central, neural canal is bounded ventrally[1] by the dorsal[1] face of a large bony cylinder, the *centrum*, and on all other sides, by the *neural arch*, which projects dorsally as a *neural spine.* The vertebrae are separated from those above and below by thick cartilaginous pads between the centra and by smooth, cartilage-covered sliding surfaces on the neural arches. The movement between any two adjacent vertebrae is very slight, limited by strong, ligamentous bindings and intricately interlacing muscles, but the summation of the slight movements between adjacent vertebrae permits considerable flexibility to the vertebral column as a whole. Notwithstanding the basic similarity shown by all the vertebrae, the work they have to perform in the several body regions is correlated with differences in proportion and in details of their structure, so that we can distinguish 5 vertebral regions. The neck region consists of 7 *cervical vertebrae;* the thoracic or chest region comprises 12 *thoracic vertebrae,* each of which bears a pair of movable ribs; the lower trunk or lumbar region consists of 5 large *lumbar vertebrae;* in the pelvic region, 5 vertebrae are tightly fused into a *sacrum,*[2] which is rigidly attached to the pelvic girdle; and 3, 4, or 5 small vestigial vertebrae make up the *coccyx,*[3] or bony remnants of the tail.

Examined as a whole, the vertebral column in front or rear view forms a straight line, but in side view it presents definite curvatures.[4] These give it spring and resilience in walking and jumping and enable it to absorb more completely the shocks produced by these and other body movements.

The ribs of the thoracic region, together with the thoracic vertebrae, the sternum, and the cartilages that connect the anterior ends of the ribs with the sternum, form the bony framework for the walls of the thoracic cavity that encloses the heart and lungs. The basal end of each rib has two movable articulations with the vertebra that bears it, and a flexible cartilaginous connection with the sternum at its anterior end. The curved ribs not only project forward but also slant downward, with their convexities tilted slightly downward; their attachments are such that contraction of the thoracic muscles serves to lift the ribs and to rotate them slightly, thus increasing both the depth and the breadth of the thoracic cavity. This movement, together with the contraction of the curved muscular diaphragm that separates the thoracic and abdominal cavities, increases the cubic capacity of the thorax and causes inspiration of air into the lungs.

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[1] The Latin word *venter* means "belly"; hence the adjective "ventral" means the belly surface of any part, and the adverb "ventrally" means toward or in the direction of that surface, or bellyward. Similarly, the Latin *dorsum* means "back"; "dorsal" is the adjective, pertaining to the back surface, and "dorsally," the adverb, toward or in the direction of the back. In nearly all animals except man, and in man if he were to go on "all fours," "ventral" means lower, and "dorsal" means upper.

[2] Latin, *sacrum,* "sacred." There are two views as to the origin of this name. One is that it was a part of the body especially used in human sacrifices in ancient times. The other is that it came from the idea of Jewish rabbis that this bone would resist decay longer than any other and would become the "germ" from which the body would be resurrected.

[3] Greek, *coccyx,* "cuckoo." So called from its fancied resemblance to the beak of this bird.

[4] Leonardo da Vinci, sometime between 1489 and 1510, was the first to represent correctly not only the curvatures of the spine but also the tilting of the sacrum (as a result of which the weight of the trunk is brought directly over the legs) and the slant and curvature of the ribs so essential for the mechanics of respiration.

The Appendicular Skeleton. The bony framework of the arms and legs and the girdles that attach these appendages to the axial skeleton constitute the appendicular skeleton. Comparison will show that the two girdles and their appendages are built upon the same fundamental plan. There are, however, considerable differences in the sizes and shapes of the corresponding bones, and the pelvic girdle is rigidly fused to the sacrum of the axial skeleton, whereas the pectoral girdle is very loosely and flexibly joined to the thoracic portion of the axial skeleton by ligaments, cartilages, and muscles.

The Pectoral Girdle and the Arm. A pair of slender, curved, rodlike *collarbones* (clavicles) extends from the upper end of the sternum to the upper part of the shoulder. There each clavicle forms a movable joint with one of the *shoulder blades* (scapulae)—broad, flattened plates which extend from the shoulders toward the spine above the upper thoracic ribs. On the dorsal surface of each scapula, there is a flattened, projecting plate (the spinous process); the apex of this process overhangs the shoulder joint, forms the point of the shoulder, and has the clavicle attached to its inner face. Just inside the shoulder joint, the reduced remnant of a third bone is fused to the scapula, forming a projection that serves for the attachment of certain arm and shoulder muscles. The head of the *humerus,* or upper armbone, fits into a shallow socket, the *glenoid fossa,* in the outer end of the shoulder blade; the ball-and-socket joint thus formed permits great freedom of movement.

The skeleton of the arm consists of an upper arm bone, the *humerus,* two lower armbones, the *radius* and *ulna,* and the bones of the wrist and hand. The humerus forms a hinge joint at the elbow with the radius and ulna. The lower end of the ulna lies on the little finger side of the forearm, and its upper end encloses part of the end of the humerus to form the elbow. The radius, at its lower end, lies on the thumb side of the forearm; its upper end is somewhat cupped, forming a rotatable junction with a convexity at the end of the humerus that permits the

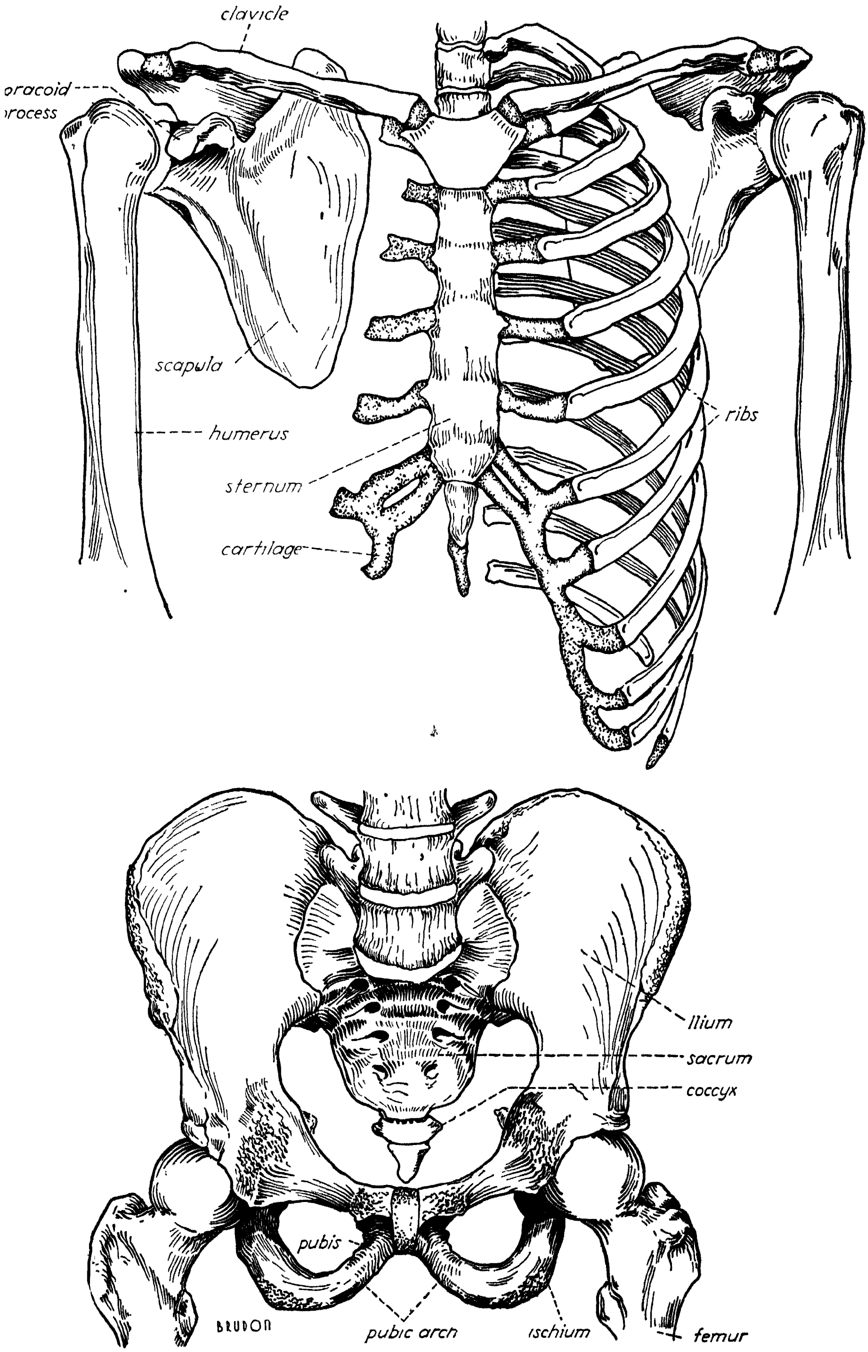
clavicle
oracoid
rocess
scapula
humerus
sternum
cartilage
ribs
ilium
sacrum
coccyx
pubis
BRUDON
pubic arch
ischium
femur

Fig. 15. *The pectoral and pelvic girdles as seen from the front (male).*

radius to move across and partly around the ulna in the familiar movement of turning the wrist (Fig. 17). The skeleton of the hand comprises eight small wrist or *carpal bones*, five long *metacarpal* bones imbedded in the palm, and the phalanges, or finger bones. There are two phalanges in the thumb and three in each of the other fingers. The human hand is essentially generalized in structure; *i.e.*, it is structurally not far removed from the basic type from which the hands and feet of all the higher vertebrates have been derived and has not become highly modified

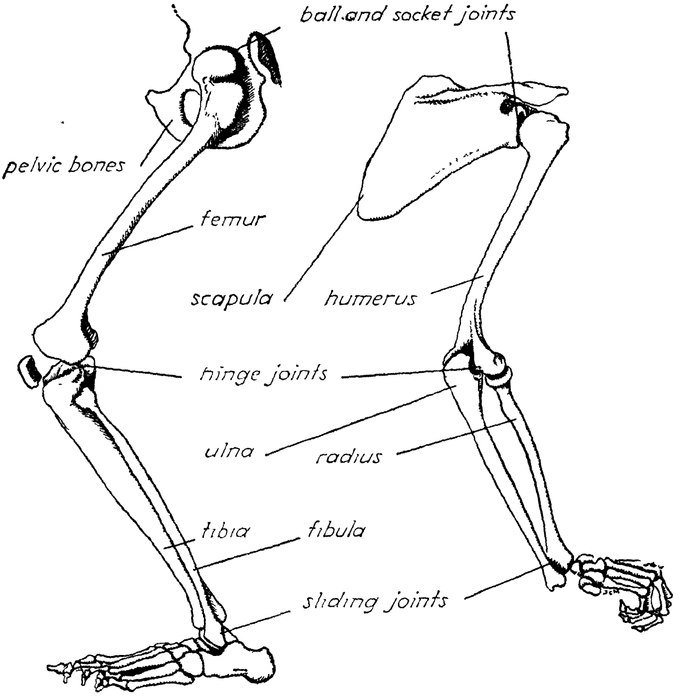

FIG. 16. *Somewhat disarticulated bones of human leg and arm, indicating three types of joints and the part-for-part correspondence in the form and arrangement of bones.*

for the performance of some particular function. Nevertheless, certain features of the hand and arm may be regarded as specializations for variety of movement and versatility of use. Such are the rotatability of the radius, the great flexibility of the fingers, and the opposability of the thumb. The general usefulness of the hand and arm of man, especially the ability to grasp and manipulate objects, has evidently had much to do with the development of his mentality and the attainment of the dominant position that he now holds in the world of life.

The Pelvic Girdle and the Leg. The pelvic girdle has the form of a large and irregularly symmetrical bony ring, made up of three pairs of strongly fused bones, having a deep socket on either side to receive the rotatable ball of the femur or thighbone. The shape of the pelvis differs slightly in the two sexes; that of the male is somewhat narrower, deeper, and more funnel-shaped, as contrasted to the wider, shorter, and shallower pelvis of the female.

The skeleton of the leg consists of a single upper leg or thigh bone, the *femur,* and two lower leg bones, the *tibia* and *fibula;* a small, separate, flattened bone forms the *kneecap.* Of the two lower leg bones, the tibia or shinbone is the larger; at the ankle the tibia is on the inner side and the fibula on the outer side of the leg. The foot is more highly modified for the performance of a specific function than is the hand but is clearly built on the same plan. The heel and ankle are made up of seven smallish bones of various sizes and shapes, collectively known as the *tarsal bones;* the largest of these (calcaneum) forms the point of the heel, and the second largest (astragalus) lies above the heel bone and articulates with the end of the tibia. In front of the tarsals are five longer bones, forming the anterior part of the arch; these are the *metatarsals.* The bones of the toes, like those of the fingers, are called *phalanges;* the great toe, like the thumb, has but two, the remaining toes, three, like the fingers. The bones of the foot are so arranged as to form three arches that aid in supporting the weight of the body. Two of these are the outer and inner longitudinal arches; the third is transverse. The highest point of the longitudinal arches lies just in front of the ankle joint, in the region of the tarsal bones. Although the bones provide the chief structural elements of these arches, it is the tight binding of ligaments and muscles that enables them to keep their shape when weight is placed upon them. The foot, in conformity with its weight-carrying function, is much stronger, more compact, and less flexible than the hand.

A comparison of the bones of the appendicular regions, outlined below and shown in Figs. 12, 15, 16, and 17, shows the principal correspondences.

Pectoral Girdle	*Pelvic Girdle*
Shoulder blade (scapula)	Ilium or hipbone
Collarbone (clavicle)	Pubis
Corocoid process of scapula	Ischium (on which we sit)
Glenoid fossa (socket for the humerus).	Acetabulum (socket for the femur)
Humerus of upper arm	Femur of thigh
Radius Ulna } of forearm	Tibia Fibula } of shank
Carpals (8) of wrist	Tarsals (7) of ankle
Metacarpals (5) of wrist.	Metatarsals (5) of arch
Phalanges:	Phalanges:
2, thumb	2, great toe
3 3 3 3 } of fingers	3 3 3 3 } of other toes

Joints. We have seen that all the bones of the head (except the lower jaw and three pairs of tiny ear bones) are immovably fused, as are the bones of the hip girdle and, in the adult, the sacrum to which this girdle is fused. Most of these immovable fusions or sutures are tremendously strong, reinforced by intricate dovetailing at the lines of juncture. Elsewhere, except for the cartilaginous union of the upper 10 pairs of ribs and collarbone with the sternum, all the joints between bones are more or less movable, and appropriate movements are provided for by smooth articular surfaces sheathed in "bearings" of cartilage and held in contact by strong ligamentous bindings.

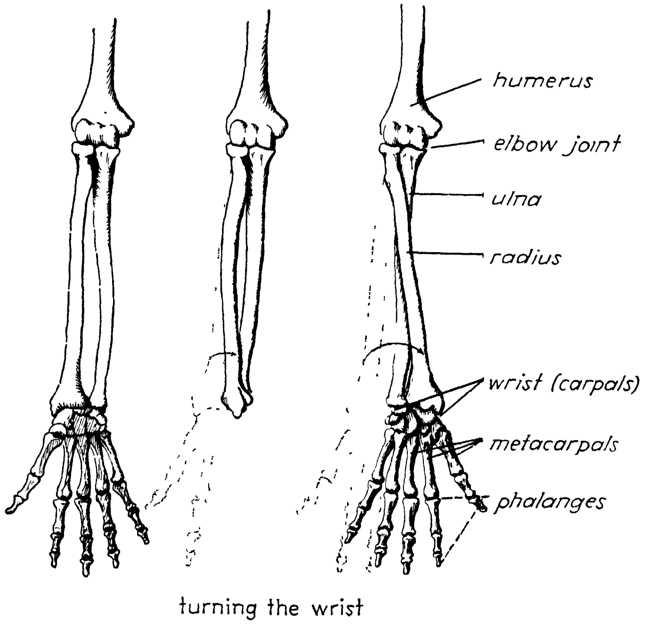

FIG. 17. *The bones of the human forearm, showing the joints and movements involved in turning the wrist.*

The variety of movable joints in the skeleton is considerable, and all are remarkably adapted for the particular requirements and necessary limitations of each particular joint. In general, although each joint has its own peculiar problems, we can recognize the *pivot joint* between the first two cervical vertebrae; the *ball and socket joints* between the humerus and shoulder girdle and between the femur and hip girdle; the *hinge joints* between the humerus and ulna and between the femur and tibia; and the *sliding joints* between most of the vertebrae and in the arch of the foot. Other joints may be of one of these types or may show combinations of hinge and sliding movements. Examine the joints shown in Figs. 16 and 17, especially the peculiar arrangement of the radius and ulna at the elbow (Figs. 17 and 18), noting the strong hinge joint between ulna and humerus and the freely rotatable connection of the radius. All joints that involve much motion are particularly adapted to reduce friction; the cartilaginous cap of each bearing surface is comparatively thick and extremely smooth, and the whole joint is bathed in a fluid contained in a surrounding capsule of fluid-tight ligaments.

The Skeletal Muscles

The active, energy-using, heat- and waste-producing part of the locomotor system is the great complex of *voluntary* or *skeletal muscles* that are attached to the skeleton and provide the power for its movements. Later we shall encounter other types of contractile tissue (heart muscle and involuntary, visceral, or smooth muscle) as parts of the circulatory, digestive, reproductive and other body systems.

As has already been mentioned, the skeletal muscles account for the greater part of the weight and bulk of the human body. They are made up largely of a type of contractile tissue known as *voluntary* or *striated muscle,* which shows the highest adaptation of all contractile tissues for rapid and powerful movement. The familiar "meat" of our diet consists to a great extent of the skeletal muscles of other animals. A slice of round steak or ham is a section of the large leg muscles of a cow or pig, together with portions of bone and connective tissue.

Nearly all skeletal muscles are attached to bones in such a way as to bring about movement of parts of the skeleton when the muscles contract. Frequently the bone serves as a lever; thus, in the instance of the forearm, the elbow is the fulcrum, the force is applied beyond the elbow, at the point of muscle insertion, and the action is that of a lever of the third class. The muscle works at a mechanical disadvantage and must exert a force of many pounds to lift a weight of a few pounds held in the hand. On the other hand, the muscles are able to move the forearm rapidly and to carry the hand through a wide arc while they themselves shorten by only a few inches.

The Structure and Functioning of the Biceps. As an illustration of a typical skeletal muscle, we may consider the *biceps*, one of the larger muscles of the upper arm. The biceps is attached at its upper end by two tendons,[1] one to the shoulder blade and the other to the end of the humerus, just below its joint with the scapula. The lower end of the biceps is attached by another strong tendon to the upper end of the radius of the lower arm, so that when the muscle shortens, it pulls the radius upward, bending the arm at the elbow. In normal arm movements, many other muscles cooperate in this action. We speak of the relatively immovable anchorage of the one end of a muscle (in this case, at the shoulder) as the *origin*, and of the attachment to the normally moved part (here the radius) as the *insertion;* the movement that results from the shortening of the muscle is known as its *action*, in this case the bending and/or lifting of the elbow.[1] If we look at the biceps in some detail, we find that it is covered with a tough, smooth, connective-tissue sheath that allows it to slide and move over other muscles without friction and that binds its parts together. We note also that the muscle is thickest near the middle and tapers toward either end. If we now cut the muscle in two across its middle, we find that the circular surface of the cut end shows a structure somewhat like that shown in Fig. 19. It is at once evident that the muscle is not entirely composed of a single kind of tissue—in fact, as was pointed out in a previous discussion, a skeletal muscle constitutes an organ, in which various tissues contribute toward the performance of a particular function. Within the outermost sheath of connective tissue, there are a number of smaller compartments or bundles (*fasciculi*), surrounded by connective-tissue walls. These, in turn, are composed of still smaller bundles, surrounded by

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[1] The two "heads," each with its own tendon, account for the name *biceps*.

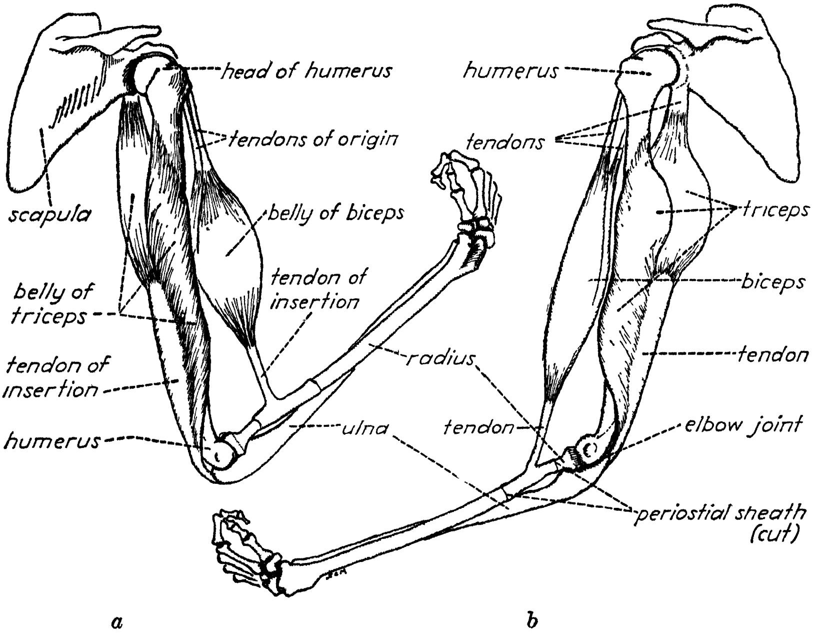
head of humerus
tendons of origin
scapula
belly of biceps
belly of triceps
tendon of insertion
tendon of insertion
humerus
radius
ulna
humerus
tendons
triceps
biceps
tendon
tendon
elbow joint
periostial sheath (cut)
a
b

FIG. 18. *Muscles and bones of the arm, showing the action of antagonistic sets of muscles. (a) Flexing; (b) extending.*

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[1] Depending upon what other muscles cooperate with the biceps in producing the action.

connective tissue; and each of the latter (Fig. 20), when teased out beneath the microscope, is found to contain many elongated, closely fitting muscle cells. Each elongated cell is somewhat spindle-shaped and, unlike most other cells, contains a considerable number of nuclei. Inside the cell membrane, we find many slender, threadlike strands running from end to end of the cell, bathed in a much thinner fluid that fills all of the rest of the cell space. Each minute thread or strand (*sarcostyle*) is made up of long series of alternating blocks of different material

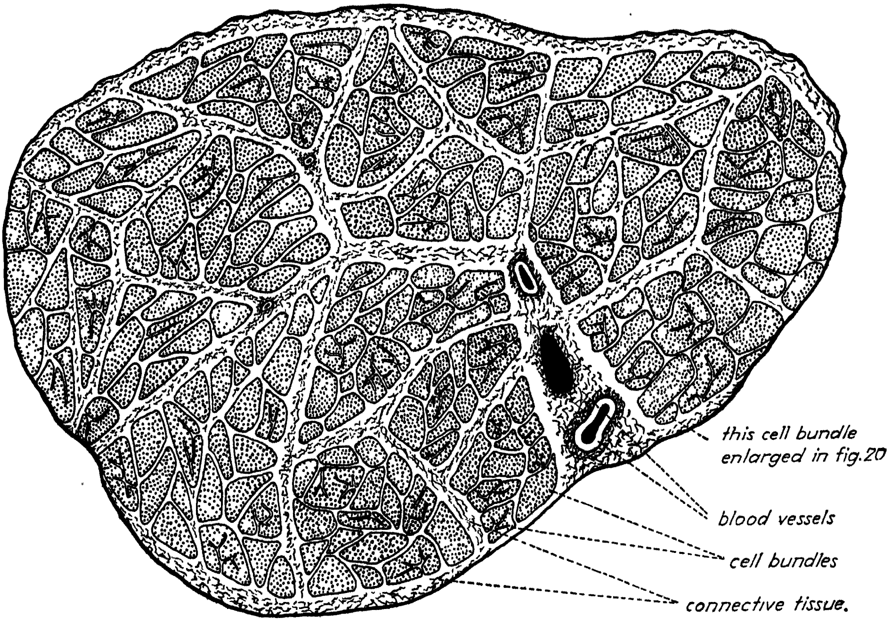

FIG. 19. *Cross section of a human skeletal muscle showing the arrangement of cell bundles. (Redrawn from Maximow, Textbook of Histology, W. B. Saunders Company.)*

so that the whole thread, if greatly magnified, looks somewhat like a long string of alternating beads. It is these alternating blocks, precisely "dressed upon" each other, that give voluntary muscle its cross-striped or striated appearance (Fig. 6).

The finer structure of the muscle cell is so minute and the sequence of events that takes place at each contraction so complex that many of the details are still in question or dispute, but the following brief account is accurate as far as it goes. Each muscle cell receives the end of a tiny motor nerve that comes from the central nervous system; and when a nerve impulse comes into the muscle cell, each of the minute, string-of-beads-like sarcostyles instantly contracts, simultaneously with the occurrence of a sudden, explosionlike, energy-releasing change of an energy-storing substance in the sarcostyles. If only a single nerve impulse is received, relaxation follows immediately, and the contracted threads quickly resume their former shape. The whole performance is completed in a few hundredths of a second, relaxation taking a somewhat longer interval than contraction. In life, no voluntary movement is quite so simple; even the quickest and briefest movement is due to a stream of nervous impulses sent into the muscle, several hundred to the second, keeping the muscle in a continuous state of contraction until the series of impulses ceases.

Whatever may be the actual chemical and physical steps involved (and these are still very imperfectly understood), it is clear that the muscle stores energy in advance, all ready for use, and that the contraction of the muscle is caused by the release of this stored energy in response to nerve stimuli. Without pressing the analogy too far, one may compare the storage and release of energy in a muscle with that in a compressed air tool. The potential chemical energy of the "explosive substance" in the muscle fibers may be compared to the air pressure in the tank; the nerve impulse, to the trigger that releases compressed air into the tool; and the contraction of the muscle, to the action of the tool. Both muscle and tool can continue to operate until their stored energy is exhausted and must then have it replenished before they are able to perform more work. In the case of the air tool, the pressure in the tank is restored by a pump driven by some outside source of power; in the case of the muscle cell, the "explosive substance" is built up anew by the expenditure of energy derived from the oxidation of food in the cell.

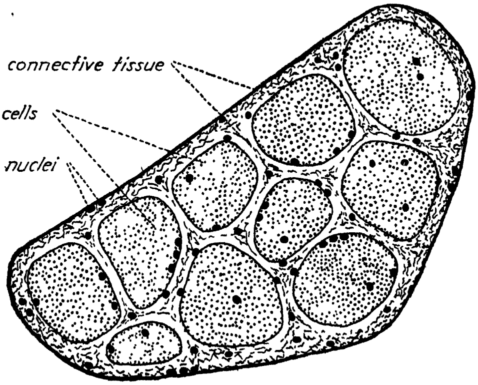

FIG. 20. *Cross section of a single cell bundle from the muscle of Fig. 19, enlarged to show cell detail. (Redrawn from Maximow, Textbook of Histology, W. B. Saunders Company.)*

One of the products of the breakdown of the "explosive substance" is lactic acid, which can be secured from muscle after action. In ordinary exercise, this acid is quickly built back into the "explosive substance" by energy-consuming processes in the muscle; but when a muscle is compelled to carry on excessive contraction, lactic acid accumulates faster than it can be built back into its energy-releasing precursor. In such cases, the excess lactic acid is excreted via the blood system and the kidneys, and so is lost from the body, necessitating the use of extra energy to restore the supply.

A muscle contraction is thus many-cell-powered, owing to the shortening of its individual cells. The contraction is initiated by nerve impulses, and the contracting cells are held together and mechanically coordinated by connective tissues. Just how much muscular power may be shown by the whole muscle depends upon many factors, but for any one biceps, the difference between gentle and powerful contractions is in large part a function of how many of the thousands of muscle cells are stimulated to contract. A gentle contraction utilizes only part of them, but when all contract together, the maximum power of the muscle is exerted. Even so, the biceps can perform but one useful action. It contracts and produces an "action" by pulling its origin and insertion closer together. It cannot push these points apart again. It requires the action of one or more *antagonistic muscles*, the contraction of which produces an exactly opposite effect, to restore the skeletal parts to their original position and to stretch out the relaxed muscle. In this instance, the antagonistic muscles pull the forearm down and straighten the elbow, at the same time stretching out the biceps; in this they may be aided by gravity.

The Body Muscles. The human body contains some 700 skeletal muscles, integrated into a muscular system and constructed upon the plan of *opposing and antagonistic sets* of muscles. Any movement that we can make requires one or more (usually several or many) muscles and also necessitates another set of muscles to return the moved part to its original position.[1] It is thus easy to understand, when we consider its great versatility of movement, why the human body contains many hundreds of separate muscles and why the total skeletal muscle tissue comprises much more than half of the total weight.

In addition to causing movement, the skeletal muscles have another important function—that of producing *heat*. Indeed, heat production is a nonavoidable result of muscular activity, some 70 to 80 per cent of the chemical energy that is released in the muscles being transformed into heat and something less than 30 per cent going into contractile energy.[2]

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[1] On the other hand, most muscles take part in a considerable variety of movements, the variations depending upon what other muscles cooperate to produce a given motion. Thus the biceps contributes to the bending of the arm at the elbow, to the raising of the elbow, to the underhanded tossing of a ball, etc.

[2] About the same percentage of efficiency as in a good steam or internal-combustion engine.

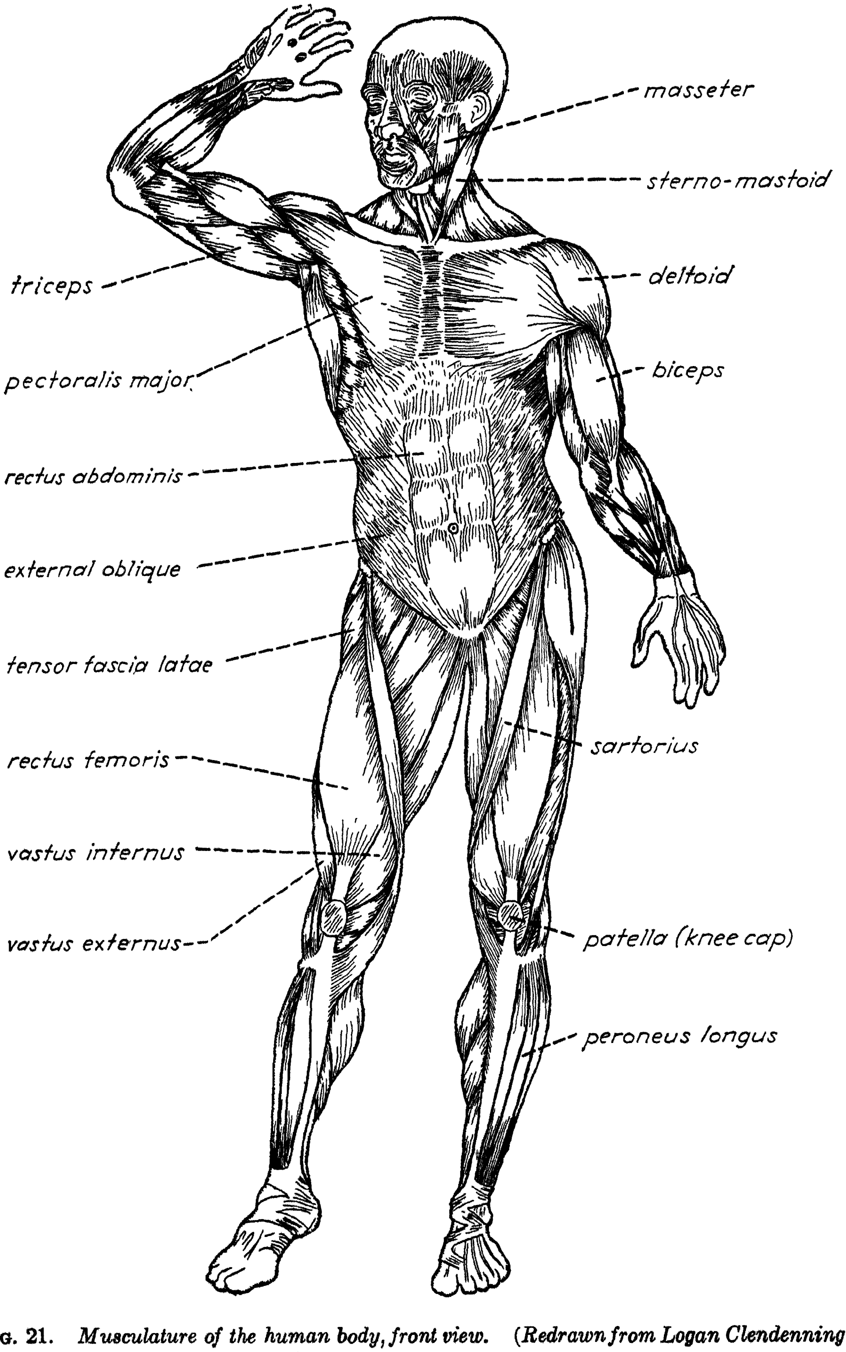
masseter
sterno-mastoid
triceps
deltoid
pectoralis major
biceps
rectus abdominis
external oblique
tensor fascia latae
sartorius
rectus femoris
vastus internus
vastus externus
patella (knee cap)
peroneus longus

Fig. 21. *Musculature of the human body, front view.* (*Redrawn from Logan Clendenning, The Human Body, Alfred A. Knopf, Inc.*)

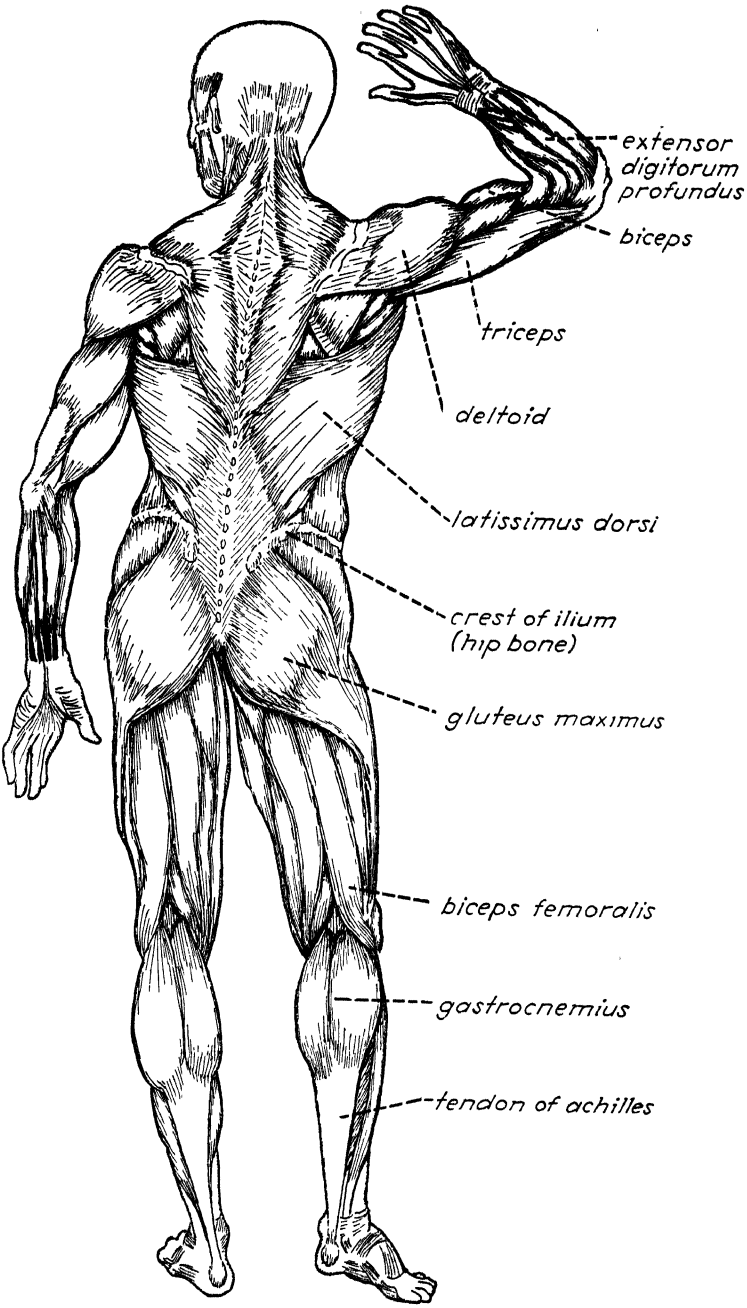
extensor
digitorum
profundus
biceps
triceps
deltoid
latissimus dorsi
crest of ilium
(hip bone)
gluteus maximus
biceps femoralis
gastrocnemius
tendon of achilles

FIG. 22. *Musculature of the human body, rear view.* (*Redrawn from Logan Clendenning, The Human Body, Alfred A. Knopf, Inc.*)

Since our bodies have a more or less constant temperature of around 98 to 99°F.,[1] enough heat to maintain this temperature is utilized and may be regarded as a useful product of muscular action; but in most climates, even moderate muscular exertion results in an excess of heat production, and this excess must be eliminated as a waste. Occasionally, when our surroundings are cold and our muscular movements have been comparatively slight, we shiver; in this case, heat production is the utilized function of muscular activity, and movement is a waste product.

Under the influence of continued exercise, the skeletal muscles increase in size and correspondingly in strength. Contrary to what might have been anticipated, this enlargement is due not to an increase in the number of muscle cells but to an increase in the size of the individual cells. Since it is a response to activity of the muscle cells and since their activity is controlled by the frequency with which nerve impulses are received, it is natural that reduction in the number of nerve impulses should have the opposite effect. If, therefore, the efferent nerve to a muscle is destroyed by accident or disease, cutting off all nerve impulses, the muscle shrinks and may ultimately disappear. The increased muscular efficiency brought about by exercise is not solely the result of the strengthening of the muscles. In even greater degree, it is due to improvements in circulatory and respiratory adjustments and better nervous coordination of muscular activity.

THE INTEGUMENTARY SYSTEM, OR SKIN

From a structural standpoint, on the basis of our definition, the skin could hardly be cited as a typical example of a "system." From the standpoint of its functioning, however, it has a much better claim to that term. Its functions are many and diverse and are grouped into the responsibility of a single system, not because they are functionally related but because all of them must be, or can be, most efficiently performed by the external body surface. They may be listed as follows:

1. To form a protection against the outside world from
   a. Mechanical injury or abrasion.
   b. Loss of water.
   c. Harmful light rays.
   d. Disease producing organisms (parasites).
2. To act as a heat-regulating and heat-eliminating organ—an efficient, thermostatically controlled radiator.
3. To house a tremendously numerous and varied set of sense receptors, capable of receiving detailed information about the body's general and detailed environment.

[1] The normal mouth temperature, marked on the clinical thermometer, is 98.6°F., but internal temperatures are somewhat higher.

4. To produce the hair and nails that form a more or less useful part of the body.

The Structure of the Skin. The skin is composed of two closely knit layers—a comparatively thin, bloodless *epidermis* and a much thicker *dermis,* crowded with blood vessels and rich in nerve endings. An examination of Fig. 23 will show the general arrangement of parts and make the following description much clearer.

The inner portion of the epidermis is a compact layer of columnar epithelial cells (*Malpighian layer*) that is everywhere in close, inseparable contact with the upper surface of the dermis. It receives a rich supply of nourishment from the blood vessels of the dermis. All through the life of the individual, cells of this inner layer of the epidermis are multiplying by cell division, and the excess cells are being pushed outward toward the surface of the skin; the many-cell-thick epidermis is thus composed of cells that are in process of being shoved to the surface, where they are constantly being worn away. As each cell progresses from the inner layer toward the surface, it becomes more and more compressed and changed in composition, until at the surface the formerly columnar cell has now become flat, thin, and lifeless and is ready to be shed from the body.

The *dermis,* which is many times thicker than the epidermis, is composed chiefly of connective tissues, through which ramify numerous small blood and lymph vessels and in which are imbedded a huge number of nerve endings, dermal sense organs, and smooth muscle cells. It is the comparatively thick, tough, outer portion of the dermis that, when tanned, is known as *leather.* The inner, less tightly compacted region of the dermis may contain many globular fat cells and is one of the principal regions for the storage of body fat.

As a receptor system, the dermis contains thousands of nerve endings for the reception of heat, cold, touch, pressure, and pain stimuli. Individual receptors for each of these sensations occur over all of the body surface, although they are much more closely spaced in some regions than in others. Touch receptors, for instance, are many times more numerous per unit of surface on the finger tips than on the back of the hand and much more numerous on the back of the hand than on the small of the back.

Some parts of the body have the skin very firmly attached to the deeper tissues, but in other regions, the skin is very loosely and movably attached, permitting free play of the enclosed parts. The skin likewise varies greatly in thickness from one region of the body to another. On the inner surfaces of the hands and the soles of the feet, there are multitudes of tiny ridges that increase friction and reduce the tendency to slip. These form the familiar fingerprint pattern and leave their traces on objects touched because of the alignment of sweat glands along the ridges. The pattern of these ridges is individually characteristic and remains constant throughout life.

Appendages of the Skin. The appendages or accessory structures of the skin are the nails, hair, glands, and teeth. An inspection of Fig. 23 will show a *hair follicle* and *root*, a *sweat gland* and an *oil gland*. It will be observed that both the hair follicle and the glands are formed by long invaginations of the Malpighian layers of the epidermis, extending deep into the dermis. Incidentally, the sweat and oil glands show two rather different devices by which an epithelium may be enormously expanded to form a many-cell-powered secreting structure.

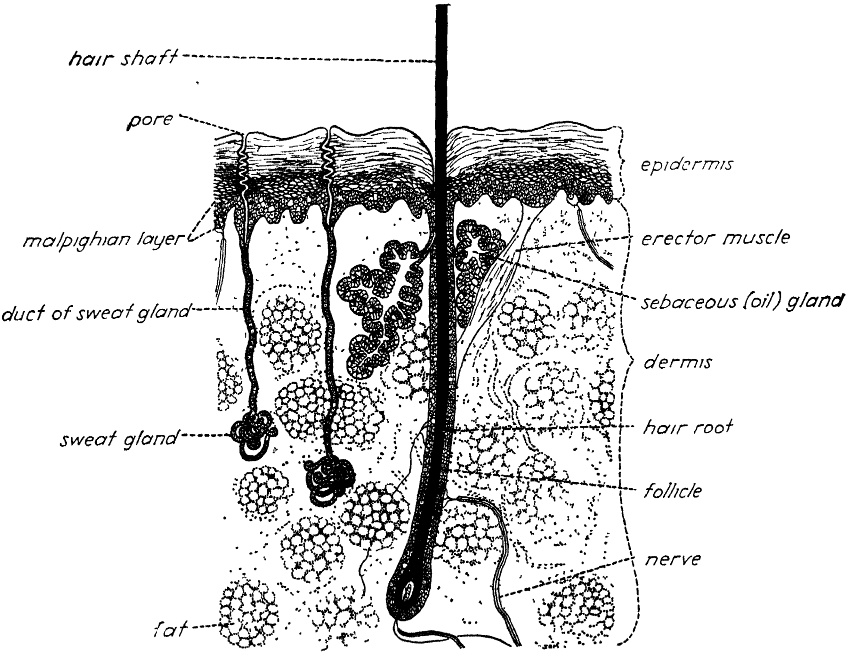

FIG. 23. *A diagrammatic cross section of the human skin. The blood vessels have been omitted. (Redrawn from Logan Clendenning, The Human Body, Alfred A. Knopf, Inc.)*

Hairs are formed by the secreting cells that line the bottoms of the deeply pitted hair follicles. The part of the hair contained within the pit is the *root;* the portion extending above the surface of the skin is the *shaft.* With the exception of the palm of the hand, the sole of the foot, and the last phalanges of the fingers and toes, the whole skin is provided with hair follicles. The nature and color of the hair in different individuals are due to details of hair growth and development that are, in part, determined by inherited factors. In general, hair grows from the bottom of the follicle, the previously secreted portion being pushed out of the follicle to project farther and farther from the surface of the skin. Loss of hair may be due to inherited factors or to disease and functional disorders.

Nails are composed of clear, horny dead cells joined to form a solid continuous plate. Nail growth is rather similar to that of hair, except that in the case of the nails, the nail-producing cells are densely packed along the invaginated furrows from which the nails are developed.

Oil glands occur everywhere over the surface of the skin except on the palms of the hands and the soles of the feet. They are very abundant in the scalp and in the face. Nearly everywhere they are associated with hair follicles. A typical oil gland is shown in Fig. 23, opening into the upper part of the hair follicle, through which its oily secretion reaches the surface of the skin to spread as a protecting oily film. This film of oil keeps hair from becoming dry and brittle and serves to prevent undue absorption or evaporation of water from the skin itself.

Sweat glands are abundant over the whole body skin but are largest and most numerous under the arms, on the palms of the hands and the soles of the feet, and on the forehead. These glands have separate openings on the skin surface, the pores, there being as many as 2½ million of these on the entire body. Sweat is, in a sense, a waste product, and sweating plays a part in the elimination of body wastes; but a much more important function of sweating is the control of body heat through the evaporation of water.

We have seen that body heat is largely produced by the muscles. This heat is taken up by the blood and distributed throughout the body, which has a normal temperature of approximately 98 to 99°F. The skin, with its abundant blood supply, is so situated that it acts as an effective heat-eliminating surface. Contraction of the muscle fibers of the dermis and of the walls of its blood vessels reduces the size of the capillaries and thus lessens the amount of warm blood exposed to loss of heat; relaxation of the muscle fibers and dilation of the blood vessels allow a more rapid loss. In addition to the considerable loss of heat by radiation, the skin is cooled by the evaporation[1] of a watery fluid, sweat, from the body surface; the amount of cooling is varied as required, by changes in the activity of the sweat glands.

Teeth. A conspicuous feature of the skull is the double row of teeth imbedded in the upper and lower jawbones, similar to bones in their hardness and appearance. Structurally, however, teeth are a part of the skin and are more comparable to such skin appendages as nails and hair than to the bones of the skeleton. Their relation to the skull is entirely secondary, their implantation in the jawbones being merely an arrangement for strength and support. Teeth, being used for the breaking up of food materials in the process of chewing, are functionally most closely associated with the digestive system.

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[1] It is this large loss of heat by evaporation that permits the human body to maintain its normal temperature, even though the air temperature may be well above 100°F.

Like other mammals, man has two sets of teeth. The temporary first set, the deciduous or "baby" teeth, are 20 in number. They are "cut" (or erupted) between the ages of six months and two and one-half years and are gradually replaced by the teeth of the second or permanent set. The latter are normally 32 in number and comprise, on each side of each jaw, 2 incisors, 1 canine (cuspid or "eye tooth"), 2 premolars (bicuspids), and 3 molars. The incisors are the "front" teeth—flat, edged, used for cutting off morsels of food; the canines are heavier and more pointed and correspond to the tearing and stabbing "tusks" of carnivorous mammals; the premolars are broad-surfaced grinding teeth with two elevated cones on the grinding surface; and the molars are larger grinding teeth with four (sometimes five) elevated cones on the grinding surface. The last pair of molars are the so-called "wisdom teeth," which in man are frequently not erupted until late in life, if at all. Since

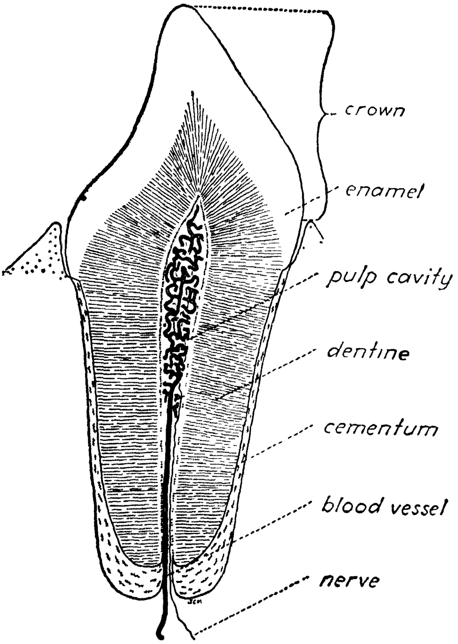

FIG. 24. *A longitudinal section through a human incisor tooth showing relations of layers and parts. (After Böhm, Davidoff, and Huber.)*

these groups of teeth are common to the mammals in general and vary in number, kind, and use from one animal to another, it is customary to express the dental armature of a given kind of mammal by means of a formula that shows the number of upper and lower teeth on one side of the jaw. The dental formula of man and of all his nearest allies is

$$I\,\frac{2}{2},\ C\,\frac{1}{1},\ P\,\frac{2}{2},\ M\,\frac{3}{3} = 16$$

The structure of a typical tooth is shown in Fig. 24. The outer layer of enamel that covers the surface of the exposed parts of the tooth is the hardest tissue in the human body.

The Skin and Disease. One of the outstanding functions of the skin is to repel the invasion of disease-producing organisms. In this respect, it plays a dual role. The first line of defense of the body is the skin surface, both because the outer part of the epidermis is tough and relatively impervious and impenetrable and because the normal skin secretions have a considerable bactericidal action. If the normally intact epidermis is injured and bacteria penetrate to the dermis, they encounter the second line of defense, provided by tremendous numbers of white blood cells that can be carried to the invaded dermis by its rich network of capillaries and lymph vessels. This will be discussed more fully in the treatment of the circulatory system.

In spite of the skin's protective ability, many plant and animal organisms have developed the capacity to live in it (*i.e.*, the fungi that cause ringworm and athlete's foot) or to penetrate it and reach the internal organs (*i.e.*, the larvae of hookworms).

CHAPTER IV

The Intake of Materials and Energy

As long as the body is alive, it requires a constant supply of materials to provide energy and to take care of growth and repair. All body energy is derived from the slow burning (oxidation) of certain food substances within the cells of the body. The materials needed for growth and repair include these same foods and, in addition, such other component parts of protoplasm and body fluids as water, various inorganic salts, and a group of special substances known as *vitamins*.

All the materials required by the body, except oxygen, are taken into it by way of the *digestive system;* the intake of oxygen is provided for by the *respiratory system.*

FOOD MATERIALS

Food may be so defined as to include all the essential materials taken into the digestive system. In this sense, the term includes proteins, carbohydrates, and fats, and also water, a considerable list of inorganic salts, and the vitamins. In a narrower sense, we may restrict the term *food* to those substances which not only are required for the building up of protoplasm but which are also capable of being oxidized to provide energy. It is the substances of this last class, comprising the proteins, carbohydrates, and fats, that commonly occur in nature in a condition unsuitable for direct passage through cell membranes and hence require a digestive process before they can be taken into the cells or blood stream and become available for use.

Carbohydrates contain carbon, hydrogen, and oxygen, usually with the hydrogen and oxygen in the same proportion as in water (H_2O). Glucose (dextrose or grape sugar), $C_6H_{12}O_6$, is an example. It is readily soluble in water and will pass through a cell membrane. Carbohydrates with this chemical formula are known as *single sugars*, or monosaccharides. Disaccharides—for example, cane sugar—have the formula $C_{12}H_{22}O_{11}$ and may, under suitable conditions, be split into two molecules of a monosaccharide after a molecule of water has been added. Various *polysaccharides* exist whose formulas may be expressed by the generalized formula $n(C_6H_{10}O_5)$. Starch, glycogen, and cellulose are examples. Under suitable conditions, polysaccharides may be split into monosaccharides. Carbohydrates are primarily energy foods. When a monosaccharide is oxidized in the body, energy is released, and CO_2 (carbon dioxide) and H_2O (water) are the end products.

$$C_6H_{12}O_6 \text{ plus } 6O_2 \text{ yields } 6CO_2 \text{ plus } 6H_2O \text{ plus energy}$$

Fats, like carbohydrates, are composed of carbon, hydrogen and oxygen, but much less oxygen is present in proportion to the carbon and hydrogen. As in the case of carbohydrates, oxidation of fats results in the release of energy and production of carbon dioxide and water. However, more oxygen is required to oxidize a fat than is necessary to oxidize a carbohydrate, and the energy derived from the oxidation of fat is correspondingly greater. The energy value of fats in human metabolism is about two and one-fourth times that of carbohydrates. Fats are stored as such in many parts of the body, especially in the deeper layer of the skin and around the intestines.

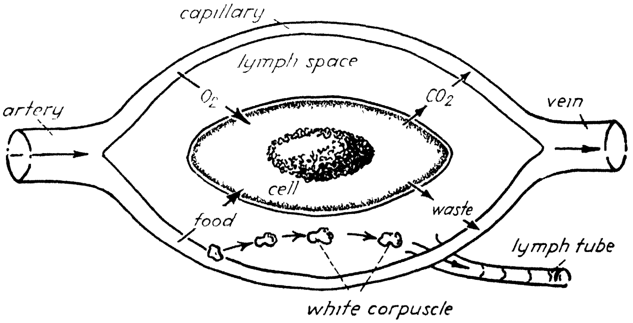

FIG. 25. *Diagram of a cell in relation to artery, capillary, vein, and lymph vessel, to show intake of oxygen and food, and outgo of carbon dioxide and metabolic wastes.*

Proteins contain nitrogen and sulphur and sometimes other elements in addition to carbon, hydrogen, and oxygen. Proteins cannot pass through cell membranes; under suitable conditions, however, they can be split into amino acids and in this condition become available to the cell. The amino acids are the building stones from which proteins are constructed. They are nitrogenous derivatives of the fatty acids. Glycine, $CH_2.NH_2.COOH$, is an amino-acetic acid, and the simplest member of the amino-acid group. At least 23 such acids are known, some of which are more important in human physiology than others. The various amino acids are combined in the cells to form the particular proteins required by each cell. There is little storage of excess proteins in the body tissues, and new supplies are therefore constantly needed. Proteins are essential for growth and repair, but they may also be used for fuel.[1]

Vitamins. Vitamins are a varied group of organic substances, required in very small amounts, but essential to the maintenance of the body. They are used in such small quantity that they cannot be a source of energy; their importance lies in the fact that they are necessary either for the proper development of various organs or for the successful performance of certain body functions. Recognition of the existence of these substances has come from the study of disease or malfunctioning associated with some type of diet and found to be curable by some other type of diet. By chemically fractionating the curative diet and determining which of the resulting portions has retained the curative properties, it has been possible gradually to narrow the search, until today many of the vitamins have been isolated and their chemical formulas determined. Much of the experimental work has been done with laboratory animals, and the results have later been found applicable to man.

The very existence of vitamins as such was unknown prior to 1881, and most of our knowledge about them has been gained within the past 30 years. The name "vitamin" is a slight modification of vitamine, a term invented in 1913 under the erroneous impression that these substances belong to a group of chemical compounds known as "amines." With the dropping of the final *e* to prevent this mistaken chemical identification, the word "vitamin" has now become established in scientific and popular usage.

Although knowledge of vitamins is so recent, certain human diseases had long previously been ascribed to deficiencies in diet. It had been found by experience that rickets could be cured by liver or liver extract; beriberi, by rice polishings; and scurvy, by fresh fruit, especially the juice of limes and lemons. Between 1907 and 1920, it was determined that rickets (and night blindness), beriberi, and scurvy were specifically caused by deficiencies in three dietary factors. These, because their chemical nature was unknown, were called, respectively, vitamins A, B, and C. Since 1920, the discovery of additional vitamins has been rapid, and the original vitamins A and B have been found to be complexes of vitamins, related but having distinct properties. By 1940, 10 different vitamins had been recognized in the B complex, and the old vitamin A had been subdivided into A, D, and E; of the three vitamins originally recognized, only vitamin C remained undivided.

Some of the vitamins (B and C) are water-soluble; the others (A, D, E, and K) are fat-soluble. The chemical formulas of many of them have been determined, and today they are as often called by their chemical as by their alphabetic names. With the discovery of their chemical constitution, it became possible to make some of the vitamins synthetically, and seven of the more important ones are now available as drugs, either as concentrates from natural sources or in synthetic form. At present, the following eight vitamins are known to be of importance in human metabolism:

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[1] The nitrogenous part of the proteins is not utilized for fuel but is excreted as a waste product by way of the kidneys.

Vitamin A
Vitamin D } from the original vitamin A complex
Vitamin E
Thiamin (vitamin B_1)
Riboflavin (vitamin B_2 or G) } from the original vitamin B complex
Nicotinic acid
Vitamin C
Vitamin K

Vitamin A ($C_{20}H_{29}OH$) is formed in our bodies from an essential precursor, *carotene.* The latter is a yellow or yellowish-orange pigment found in a wide variety of plants, especially abundant in carrots; it also forms the yellowish-orange pigment in cream, butter, egg yolk, etc. Cod-liver oil and other fish-liver oils contain the vitamin already elaborated and available for immediate use. Excess vitamin A is stored in the liver. Deficiency in vitamin A manifests itself chiefly in malfunctioning of the skin and in a condition known as *night blindness.* The vitamin evidently plays some essential role in the formation or functioning of epithelial tissues, especially the mucous membranes; in cases of marked deficiency, the skin may become hard and horny, the protective secretions diminish, and skin, throat, nose, and lung infections are apt to follow. Vitamin A also affects the formation of tooth enamel and is involved in normal body growth. Night blindness is the relative inability to see under twilight conditions, as in a partially darkened room. In the normal eye, exposure to light causes breakdown of a substance in the retina called *visual purple,* with resulting stimulation of the visual receptors, but this substance is quickly built up again from vitamin A and a protein when light intensity decreases.[1] Inability to re-form this substance rapidly causes night-blindness. This condition is sometimes an inherited defect, but is more commonly the result of vitamin A deficiency, being often the earliest symptom and one that is easily recognized.

Vitamin B of the old terminology is now recognized to have been a complex of at least 10 distinct vitamins, 3 of which are of especial importance.

Thiamin (vitamin B_1), $C_{12}H_{17}N_4OS$, is abundant in yeast and in the germ and outer layers of seeds; it also occurs in nuts, legumes, most vegetables, eggs, pork, liver, and the organs and muscles of many animals. Being water-soluble, it is often lost in cooking. This vitamin is required in only small quantities but must be constantly taken into the body, since little of it is stored. Thiamin deficiency is the most prevalent vitamin lack among human beings and seems especially common in warm countries, including the southern United States. Slight to moderate deficiency is marked by many functional disturbances, including nervousness, fatigue, and poor circula-

[1] According to Detwiler (*Sigma Xi Quarterly,* vol. 29, pp. 112–129, 1941), vitamin A is the direct precursor of visual purple and is the product of its decomposition under the influence of light.

tion in the extremities; continued, it may result in painful neuritis. Complete lack of the vitamin causes *beriberi*, a wasting disease of the skeletal muscles due to malfunctioning of the circulatory system and nerves. This condition, which is fatal if not checked, was first known (and named) in the East Indies, where polished rice forms the chief article of diet. Such rice has had the vitamin-bearing seed coat and germ removed by milling.

Riboflavin (vitamin B_2 or G), $C_{17}H_{20}N_4O_6$, occurs as a yellow pigment (different from carotene) in plant and animal tissues. The common sources are yeast, milk, liver, wheat germ, eggs, cheese, green vegetables, and muscles of animals. It is important in normal growth and appears to be concerned in the oxidative processes of cells. Deficiencies of riboflavin are not common, but when they do occur, normal nutritional and growth processes are upset.

Nicotinic acid ($C_6H_5O_2N$), another member of the vitamin B complex, has been confused with riboflavin (B_2), to which it is closely related and in association with which it occurs. Although known for some 60 years as an organic compound derived from nicotine, its role as a vitamin has only recently been established. It appears to be abundant in yeast, fresh vegetables, and lean meats—the same sources that supply riboflavin. A few injections of nicotinic acid will cure the formerly dreaded southern disease known as *pellagra*, which was prevalent in areas where "white meat" and corn bread furnished the bulk of the diet. The corresponding deficiency disease in dogs is known as *blacktongue*.

Vitamin C (ascorbic acid), $C_6H_8O_6$, is one of the oldest known vitamins and the only one of the three originally recognized that has not been subdivided. It is found in fresh fruit and fresh meat and can apparently be synthesized by many animals, although not by man. Since it is very easily destroyed by cooking, raw fruits or vegetables are required as a part of the diet. Slight deficiency of this vitamin produces general loss of energy and a variety of unpleasant symptoms, marked deficiency results in the condition known as *scurvy*. This disease, characterized by swelling gums, loosened teeth, stiffened muscles and joints, and bleeding, has a long record in medical history as one of the to-be-expected horrors of sieges and prolonged voyages. The English, long before vitamins were ever heard of, found that the use of fresh fruit or lemon juice in the navy rations would prevent or minimize scurvy.

Vitamin D ($C_{27}H_{43}OH$) is produced in the human body under the influence of sunlight. When ultraviolet rays fall upon a substance known as *ergosterol*, it is changed into another substance, *calciferol*, which appears to be the actual vitamin. Ergosterol occurs in animal oils and in the human skin, and exposure to sunlight or to the radiation of an ultraviolet lamp causes its transformation into the vitamin. Fish-liver oils are very rich in both ergosterol and calciferol, and the vitamin is also present in eggs, butter, and milk but does not occur in plants. Vitamin D may be stored in the body (chiefly in the liver) during the months of intense sunshine, forming a reserve for winter use. Unless an adequate amount of vitamin D is present in the body, calcium and phosphorus cannot be absorbed properly from foods. Marked deficiency of the vitamin results in a lack of calcium, which in children takes the form of rickets, the growing bones being bent and deformed. Vitamin D is one vitamin, at least, in which over-dosage is possible, sometimes even resulting in death from partial calcification of the kidneys.

Vitamin E ($C_{29}H_{50}O_2$) occurs in the oils of plant seeds and in some green, leafy vegetables. Wheat-germ oil is a concentrated source. In rats, the absence of this vitamin results in sterility, caused by the degeneration of the reproductive glands and even of the developing embryo. The effect of vitamin E deficiency in man is not so clearly established, though it is probable that it is required by all mammals, and some doctors have reported it useful in treating cases of human sterility. Lately it has been shown that in experimental animals vitamin E is necessary for the development of normal muscular structure.

Vitamin K ($C_{17}H_7O_2$-R) is one of the most recently discovered vitamins. It appears to be required for the formation of prothrombin—a substance found in the blood that enables it to clot and prevents death from hemorrhage. Vitamin K occurs in association with vitamin C in a variety of foods and is manufactured in the human intestine by bacterial action.

Inorganic Materials. Besides proteins, fats, carbohydrates, and vitamins, the body requires a number of inorganic substances. Chief of these is water, which forms something over 60 per cent of the body weight and is an essential part of protoplasm and all body fluids. It is also the solvent and carrier of excreted wastes and is evaporated in the maintenance of proper body temperature. The other inorganic materials essential to the body include chlorides, sulphates, and phosphates of potassium, sodium, calcium, and magnesium, as well as somewhat lesser amounts of iron.

Diet

The sum of the food materials taken in by an animal over a specified period of time makes up its diet. As was pointed out above, the requirements of the individual include materials to be burned as fuel; materials for building and repairing cells; inorganic substances to be used as structural elements, as solvents, as cooling agents, or for other purposes; and certain special substances (the vitamins) required for proper functioning of the organism. For an animal simply to eat until its hunger is satisfied is no guarantee that its diet meets all these requirements. Cattle in southern Florida, eating their fill of the lush pasturage, fell ill by the thousands of a disease called "salt-sick." They were actually starved for certain minerals lacking in the soil and hence in their food. Man, omnivorous in his food habits, would seem much less likely to suffer from dietary deficiencies; but actually, from choice or necessity, he very often does so. It will be of interest to consider briefly the kinds and amounts of food that are required adequately to maintain the human organism under various circumstances.

It is estimated that an ordinarily active man weighing 150 pounds needs enough food to yield approximately 3,000 Calories[1] of heat per day. If he is engaged in hard physical work the Calorie requirements may be as great as 5,000 or even 6,000 per day. Obviously the age, sex, weight, and activity of an individual, as well as the climate in which he lives, enter into a determination of his Calorie requirements. A two-year-old child may need only 900 Calories per day; an average woman needs about 2,100.

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[1] A Calorie, spelled with a capital letter, is the great calorie—the amount of heat required to raise 1,000 grams (1 liter) of water 1°C.

In addition to the fats and carbohydrates that are the chief energy-producing foods, the diet must include proteins, essential minerals, and vitamins. The proteins, as we have already seen, yield amino acids for building the new proteins needed by the cells for growth and repair. Of the 23 amino acids known, 8 are believed indispensable for human metabolism, and the diet must contain proteins from which these particular amino acids may be derived. At least 8 of the approximately 20 known vitamins are important in the functioning of the human body; and no fewer than 12 mineral substances are essential either as building materials or as chemical tools. A balanced diet is one that contains all these important food substances in the required proportions. It has been estimated that, for a person whose total food requirements per day average about 2,700 Calories, the ideal distribution of food materials would be as follows:

Food materials	*Grams*	*Calories per gram*	*Total Calories*
Carbohydrates	333	4	1,332 (energy foods)
Fats	100	9	900 (energy foods)
Proteins	120	4	480 (growth, repair, energy)
Minerals[1]	Small amount	0	0 (various)
Vitamins[1]	Trace	0	0 (proper functioning)

[1] Sufficient fresh vegetables, etc., to furnish these items of the diet are also required.

DIGESTION AND THE DIGESTIVE SYSTEM

Except oxygen, all the essential supplies needed for maintenance and growth enter the body by way of the digestive system. Water, salts, and most of the vitamins require no special process to prepare them to pass through the walls of the intestine. For them the digestive system merely provides a sufficient area of permeable surface through which they may pass into the blood and lymph of the circulatory system. The carbohydrates, proteins, and fats, on the other hand, are taken into the digestive tract in a form in which they cannot pass through the intestinal walls and must be first digested (broken down) into simpler substances—monosaccharides, amino acids, and fatty acids and glycerol.

Digestion involves both mechanical and chemical processes, the latter chiefly of a type known as *enzyme action.* Enzymes, sometimes termed *organic catalysts,* have the power to hasten enormously certain chemical reactions that otherwise would take place very slowly. The digestive enzymes act upon the carbohydrates, proteins, fats, and certain of their derivatives and break them down into simpler chemical compounds until the final products are able to permeate the walls of the intestine. This process is greatly facilitated and quickened by the mechanical maceration that is also a part of the digestive process. The complete process and the structures that accomplish it can be best described by following the sequence of events when a meal is taken into the digestive system.

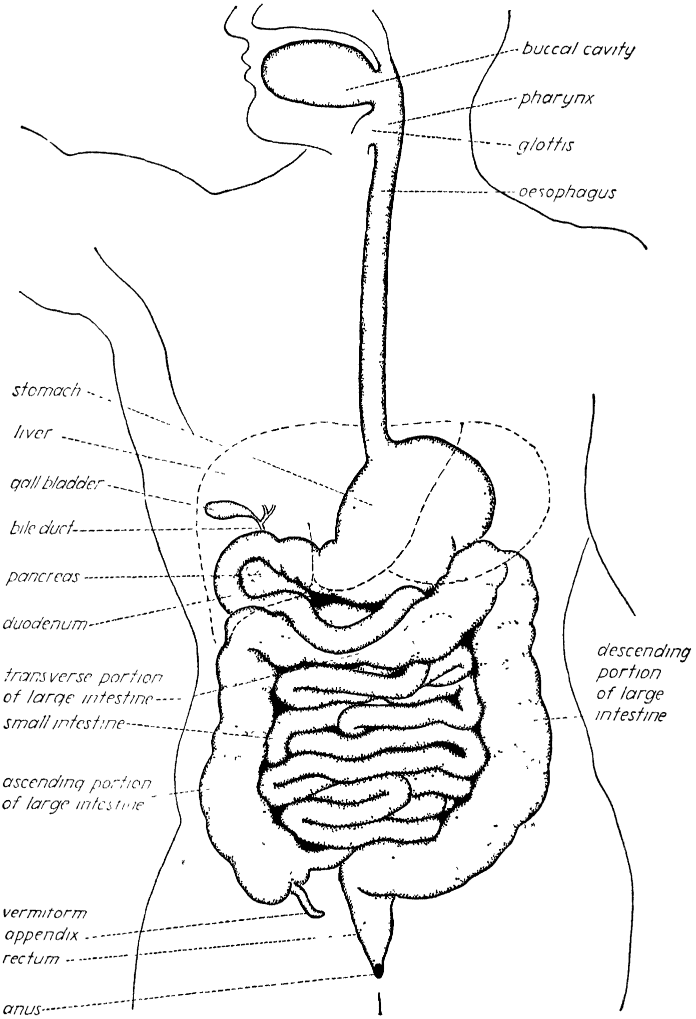
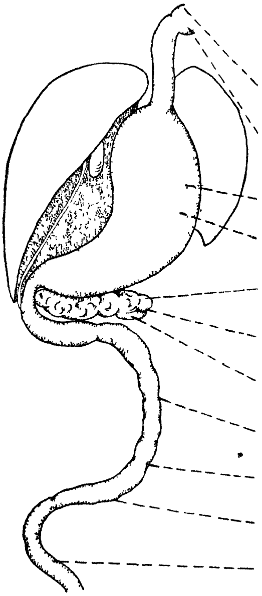

buccal cavity
pharynx
glottis
oesophagus
stomach
liver
gall bladder
bile duct
pancreas
duodenum
transverse portion of large intestine
small intestine
ascending portion of large intestine
vermiform appendix
rectum
anus
descending portion of large intestine

FIG. 26. *The digestive system, superimposed upon an outline of the human body to show the organs in their approximate location and relationship.*

The Mouth and Esophagus. Digestion and the digestive system begin with the mouth. As the food is chewed, it is mixed with *saliva,* the watery product of three pairs of mouth glands. Saliva is nearly neutral in reaction and contains two enzymes, *ptyalin* and *maltase*, which act upon certain of the carbohydrates. Chewing not only permits carbohydrate digestion to begin but prepares the food for swallowing by breaking it into smaller pieces and forming it into an easily swallowed paste. The voluntary muscles of the tongue and pharynx perform the action of swallowing, *i.e*, passing the food through the pharynx into the esophagus. (Since the pharynx is a common part of both the digestive and pulmonary systems and a passageway for both food and air, the air passages that connect with the pharynx are closed in the act of swallowing; the posterior ends of the nasal passages by the soft palate; and the opening of the upper end of the windpipe by a lid, known as the *epiglottis*.)



Gland source	Enzyme	Food affected	Product
salivary	ptyalin	starch	maltose
salivary	maltase	maltose	monosaccharides
gastric	pepsin	protein	peptones and proteoses
gastric	rennin	milk protein	coagulated milk
pancreatic	steapsin	fats	fatty acids and glycerol
pancreatic	amylopsin	starches and glycogen	disaccharides
pancreatic	trypsin	protein	polypeptids and amino acids
intestinal	erepsin	peptones, proteoses, polypeptids	amino acids
intestinal	maltase	maltose	monosaccharides
intestinal	lactase	lactose	monosaccharides
intestinal	invertase	sucrose	monosaccharides

FIG. 27. *Tabular summary of digestion in man.* (*Modified from Miller and Blaydes, Methods and Materials for Teaching the Biological Sciences.*)

The wall of the esophagus, like those of the stomach and intestine that follow it, is composed of five layers of tissue. There is first an inner epithelial layer, called the *mucosa;* this is surrounded by a layer of connective tissue, the *submucosa;* then come two layers of *smooth* (*involuntary*) *muscle tissue;*[1] and finally, on the outside, there is a smooth, thin, moist epithelium, known as the *peritoneal layer.*[1] Like the stomach and the small and large intestines, the esophagus is a tube; but unlike the stomach and intestines it is a relatively flabby, thin-walled tube, producing no enzymes and serving merely to connect the mouth with the stomach.

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[1] The muscles of the walls of the digestive tract are typical of *visceral muscle* in general. The cells making up this type of contractile tissue are flattened and spindle-shaped. Unlike skeletal muscle cells, they possess only a single nucleus and are not

Digestion in the Stomach. The swallowed food is not retained in the esophagus but passes immediately into the stomach, which is closed at its lower end by the *pyloric valve,* a sphincter muscle at the juncture of the stomach and small intestine. The food is retained in the stomach for some time—usually from 3 to 4½ hours in the case of an ordinary mixed meal. Fluids and semifluids commence to leave the stomach almost immediately after being swallowed. On account of the rates at which they are liquefied, carbohydrate leaves more rapidly than protein and protein more rapidly than fat. While the food is in the stomach, a number of important digestive processes take place.

The mucosa of the stomach contains a multitude of glands that, when stimulated, pour their secretion, the *gastric juice,* into the cavity of the stomach. This gastric juice contains *hydrochloric acid* and three enzymes. The most important enzyme is *pepsin,* which aids in the digestion of proteins. The others are *rennin,* which coagulates milk, and small amounts of *lipase,* which aids in the digestion of fats. The walls of the stomach also secrete *mucin,* a slimy and viscous substance that coats the wall of the stomach and helps to protect it against the action of the gastric juice.

The muscle layer of the stomach is thick and powerful and forms the greater part of the thickness of the stomach wall. During digestion, waves of muscular contraction begin in the region of the broad upper or cardiac end of the stomach and sweep toward the narrow lower or pyloric

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striated—*i.e.*, they do not possess the cross-bandings so typical of skeletal or voluntary muscle. For this reason, visceral muscle is often called *smooth muscle,* as opposed to striated.

Most of the internal organs of the body are essentially tubular in construction, and the walls of these tubes usually possess an outer layer of longitudinal smooth muscle, surrounding an inner and heavier circular layer. Contraction of the longitudinal layer shortens and thickens or expands the tube; contraction of the circular layer thins and elongates it. These muscles, therefore, are arranged in opposing sets like the skeletal muscles, though they are not attached to bony levers.

Compared to the action of skeletal muscles, the contraction of smooth muscles is slow and prolonged, that caused by a single stimulus lasting some 20 seconds. The action of the visceral muscles is controlled by the autonomic division of the nervous system and is not conscious; these muscles are therefore often called *involuntary muscles.*

[1] In the neck region, before the esophagus enters the body cavity, the outer layer is formed of connective tissue rather than of peritoneum. In general, the peritoneum not only forms the outer covering of the portions of the alimentary canal lying within the body cavity but lines the entire wall of the body cavity as well.

end, becoming increasingly powerful as they proceed. There may be several of these waves in progress at one time. Thus the contents of the stomach are kneaded, and the food is mixed with the gastric juice. The effect of the mechanical processes is to break up and liquefy the solid food. The chemical part of gastric digestion consists chiefly of breaking down the proteins into intermediate products (peptones and proteoses) by the pepsin[1] of the gastric juice.

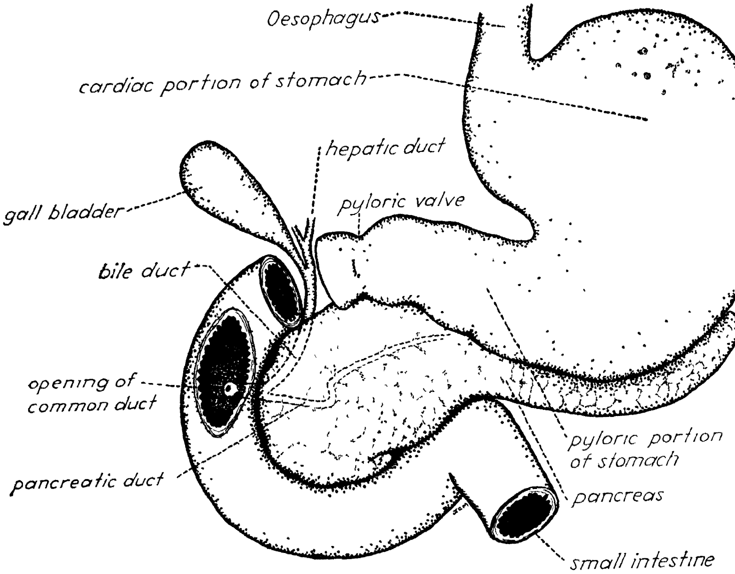

FIG. 28. *Diagram to show the relationships of the pancreas and its duct, and the ducts from the liver and gall bladder to the small intestine.*

The food next to the stomach walls is digested and liquefied first, and only gradually does the acid gastric juice penetrate to the center of the food mass. Parts of the mass remain slightly alkaline for half an hour or more, on the average, and so long as this reaction persists, carbohydrates continue to be digested by ptyalin. As gastric digestion proceeds, the contractions of the stomach squeeze the outer and more fluid portion of the stomach contents toward the pylorus. Each wave of contraction sweeps a jet of the liquefied food (*chyme*) through the relaxed pylorus into the small intestine; the pyloric valve then closes briefly and opens again at the approach of the next wave.[2]

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[1] This digestive enzyme is secreted as *pepsinogen* (an inactive precursor of pepsin, which does not attack the proteins of the gland cells); pepsinogen is changed to active pepsin by the hydrochloric acid in the cavity of the stomach. The stomach walls, as noted above, are protected by their coating of mucin.

[2] An earlier hypothesis was that the pyloric valve remained closed most of the time

Digestion in the Small Intestine. The chyme is highly acid. Upon its entry into the normally alkaline intestine, it produces two immediate effects. The first is the production of pancreatic juice; the second the entry into the intestine of a quantity of bile. These two reactions occur in response to stimuli that are partly chemical and partly nervous. The acid chyme, coming into contact with the cells of the intestinal mucosa, causes a substance called *secretin*[1] to be liberated into the blood stream. Secretin is a hormone,[2] or chemical messenger. Carried rapidly to all parts of the body by the blood, it reaches the pancreas and liver and stimulates both these organs to secrete.

In the instance of the *pancreas*, the principal substances secreted upon stimulation by secretin are water and the inorganic constituents of the pancreatic juice. The pancreas is also under control of the *vagus nerve*, which plays a large part in many visceral reflexes, particularly in glandular control. Stimulation of the vagus nerve by the entry of chyme into the duodenum reflexly stimulates the cells of the pancreas, and this nervous stimulus is chiefly responsible for the secretion of the enzymes in the pancreatic juice.

The secretion from the pancreas (pancreatic juice) contains three important enzymes: *trypsin*,[3] which digests proteins into polypeptids or

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and that passage of food from the stomach to the intestine was controlled by the degree of acidity in the duodenum. Introduction of acid chyme was believed to cause closure of the pyloric valve or reduction in the force of the stomach contractions or both, and restoration of alkalinity in the duodenum was thought either to relax the pylorus or to increase the strength of the stomach contractions sufficiently to force a jet of chyme through it. X-ray studies of "barium meals" and work on experimental animals have made it necessary to revise this conception. It is true that any strong stimulus of the duodenum will cause contraction of the pyloric valve, and doubtless the entry of the acid chyme stimulates the brief closure mentioned above. But it is found that the pylorus is open much of the time; that experimental maintenance of constantly acid or alkaline conditions in the duodenum does not prevent the rhythmic opening and closing of the pylorus; and that a principal factor in the emptying of the stomach is the rate at which the gastric contents are reduced to a fluid or semifluid consistency.

[1] The discoverers of secretin thought that it was represented in the mucosa cells by an inactive precursor, *prosecretin*, and that the latter was changed into secretin by the hydrochloric acid of the chyme. Recent studies, however, show that secretin exists preformed in the mucosa cells, from which it can be extracted by water, alcohol, and other solvents, as well as by acid. Secretin has been obtained in pure crystalline form and proves to be a proteinlike substance.

[2] A *hormone*, or chemical messenger, is a substance which, secreted in one part of the body, is capable of regulating the functions of other parts when carried to them by the blood stream.

[3] This is secreted by the pancreas in the form of inactive precursor, *trypsinogen*, which is changed to active trypsin by an activator (*enterokinase*) that is secreted by the intestine.

even into amino acids; *steapsin*[1] (also called *pancreatic lipase*), which digests fats into fatty acids and glycerol; and *amylopsin,* which changes starches (and glycogen) into disaccharides. Other enzymes are present in the intestinal juice that is secreted by the mucosa of the intestine itself. These include *erepsin,* which acts upon the peptones, proteoses, and polypeptids to form amino acids; and the inverting enzymes—*maltase, lactase,* and *invertase*—which split the disaccharides maltose, lactose, and cane sugar, respectively, into monosaccharides.

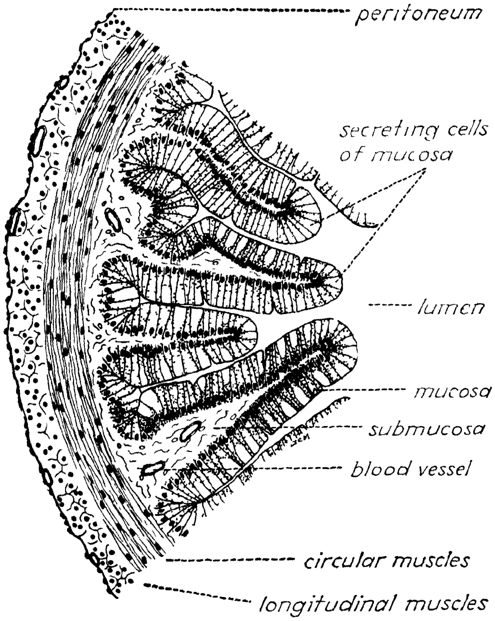

FIG. 29. *A cross section of the intestine of a frog, showing the tissues of which it is composed. The wall of the human intestine possesses the same layers, but its inner surface is much more complexly folded, and its structure is less diagrammatically clear.* (*Redrawn from Holmes.*)

Bile is secreted continuously by the liver and stored in the gall bladder; secretin merely increases the rate of its production. Discharge of bile into the intestine is caused by contraction of the walls of the gall bladder in response to stimuli produced by entry of chyme into the intestine. As in the instance of the pancreas, these stimuli are in part nervous, in part chemical. The contact of fat or of acid with the walls of the duodenum apparently liberates another hormone, related to but not the same as secretin; this hormone causes contraction of the gall bladder, forcing bile into the intestine.

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[1] Steapsin has only a weak reaction until it has been activated by the bile salts in the intestine.

Although the bile contains no enzymes, it plays an important part in digestion[1] as well as in the absorption of digested fats. In respect to both these processes, the bile salts are the effective agents. Besides activating steapsin, they emulsify the fats in the intestine, breaking them up into minute particles and enormously increasing the surface exposed to enzyme action. Indirectly they aid also in the digestion of proteins and carbohydrates by removing the fat from the surface of particles of these substances and thus exposing them to more efficient enzyme action. The role of bile in absorption is mentioned below.

The enzymes of the intestine all work best in a slightly alkaline to neutral medium; but chyme, as we have seen, is quite strongly acid. Pancreatic juice is mildly to rather strongly alkaline; bile, though quite alkaline in the liver, becomes neutral or weakly alkaline during a process of concentration that it undergoes in the gall bladder. The intestinal juice is definitely alkaline through the presence of sodium carbonate and bicarbonate. The mixing of these juices with the chyme tends to neutralize the acid of the latter and establishes a circumneutral or slightly alkaline condition that persists, with some variation, throughout the intestine.

The work of the intestinal and pancreatic enzymes is greatly facilitated by the muscular activity of the intestinal wall. The mass of food received from the stomach is pinched into numerous separate portions by local constriction of the intestinal wall, and these semifluid separate portions are shunted backward and forward, reunited and again separated by alternate contraction of the circular (constricting) and longitudinal (dilating) muscle layers. In this way, the food is much more effectively exposed to the action of the digestive fluids, and new portions are continually brought in contact with the absorptive walls of the intestine. Peristaltic waves of contraction passing along the intestine keep the food moving gradually toward the posterior end.

Digestion is completed when the proteins, carbohydrates, and fats have been broken down into amino acids, monosaccharides, and fatty acids and glycerol. As soon as these end products of digestion are formed, they, like water[2] and the salts and vitamins, tend to be absorbed through the walls of the intestine. The presence of the bile salts is necessary for the absorption of the fatty acids, with which they apparently unite; the bile salts are thus reabsorbed into the body and are eventually returned to the liver. These salts are necessary also for the absorption of carotene and vitamin D and aid in the absorption of vitamins K and E. The end products of digestion, together with the other substances mentioned above, pass through the walls of the intestinal mucosa and into the capillaries and lymph vessels of the submucosa. Once they enter the blood system, either directly or by way of the lymphatic vessels, the absorbed substances are carried throughout the body, to be taken in and utilized by the individual cells. All but a small portion of the monosaccharides, however, are taken from the blood in its passage through the liver, where they are stored in the form of *glycogen*, or animal starch.

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[1] Bile is also in part an excretion, the bile pigments representing waste products from the breakdown of hemoglobin.

[2] Some water is absorbed through the walls of the large intestine.

The Elimination of Undigested Wastes. The undigested materials that are left in the small intestine are finally passed into the large intestine.[1] The latter is much shorter than the small intestine, although distinctly larger in diameter. The undigested materials pass rather slowly through the large intestine, which "ascends" from its juncture with the small intestine in the lower right side of the abdominal cavity; crosses, at about the level of the navel, from the right to the left side; and "descends" on the left side, passing into the rectum, which terminates in the anus. The undigested waste, in its passage through the large intestine, is acted upon by a multitude of bacteria, and the fecal matter voided from the anus consists in considerable part of the bacteria that have multiplied in and considerably modified this undigested mass.

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[1] The small and large intestines do not meet end to end; the lower end of the small intestine joins the large intestine just beyond the inner end of the latter. A blind pouch (the *caecum*) is thus formed by the inner end of the large intestine. It is from this caecum that the *vermiform appendix* projects as a slender, fingerlike process.

CHAPTER V

Respiration and Excretion

FOOD taken into the body represents merely stored or potential energy. To release this energy and make it available for work, the food must be burned—*i.e.*, combined with oxygen; and this must occur within the cells that do the work. Large amounts of oxygen must therefore be taken into the body and distributed to all the cells. The supply must be continuous, for even the energy necessary for merely keeping alive comes from the burning of food, and the cells soon die if deprived of oxygen.

The oxidation of food materials not only releases energy in the form of heat and work but also gives rise to new chemical substances. Carbon dioxide and water are always produced; they are the only products of the oxidation of carbohydrates, almost the only ones from the burning of fats, and a part of the results of protein oxidation. Water is useful in the metabolism of the body; but carbon dioxide is a substance that, although necessary in minute amounts, becomes harmful if allowed to accumulate. In addition to water and carbon dioxide, the burning of proteins results in the production of nitrogenous compounds and inorganic salts that are toxic in any except low concentrations. Certain substances, notably salts, may be ingested with the food in amounts greater than can be utilized. There is also to be considered the residue of undigestible material left in the intestine after absorption of the usable parts of the food. All these useless or harmful substances must in some manner be removed from the body.

The intake of oxygen and the removal of carbon dioxide—both gases—are provided for by a single mechanism, the *respiratory system*. The food residues are eliminated by the action of the digestive canal itself. All the remaining metabolic wastes—nitrogenous compounds, excess salts, and other waste substances—are soluble solids and are disposed of in aqueous solution by the operation of the *excretory system*.

THE RESPIRATORY SYSTEM

Oxygen and Carbon Dioxide Exchange

The taking in of the oxygen needed by the body and the expulsion of the waste carbon dioxide are accomplished by a special respiratory system. This system consists essentially of (1) a large expanse of moist, thin epithelium, permeable to oxygen and carbon dioxide; (2) air passages through which the outside air reaches this epithelium; and (3) a breathing mechanism to provide continual renewal of the air in contact with the epithelial surface.

Air enters the respiratory system through the mouth or nose and, crossing the food passage in the pharynx, enters the upper end of the *trachea*, or windpipe, where the *larynx*, or voice box, a strong cartilaginous cylinder, contains the *vocal cords*. The lower end of the trachea extends into the thoracic cavity to a point somewhat below the level of the first pair of ribs, and there branches into the right and left *bronchial tubes*. Each bronchial tube leads into a *lung*, in which it branches repeatedly into smaller and smaller tubes (the *bronchioles*) until the minute terminal branchlets end in expanded air sacs (*alveoli*) of thin epithelial tissue. Each lung may be roughly compared to a huge bunch of grapes; the stem and its branches correspond to the bronchial tubes; the grapes, to the air sacs. In the lung, of course, all these structures are hollow, and the bronchial tubes show a many times more intricate and compounded branching. In addition to the structures just described, each lung contains an abundant supply of blood vessels, and is closely covered externally by a thin, moist, elastic membrane, the *pleurum*. Each lung is suspended by its root—the point where the main bronchial tube enters its medial surface—in a cavity lined by a second (outer) layer of pleural membrane.

The *thoracic cavity* is enclosed above and on the sides by the body wall; its floor is formed by the *diaphragm*, a dome-shaped muscular partition that separates the thoracic and abdominal cavities; and the cavity is divided into right and left sides by (1) a central, connective tissue framework that supports the esophagus, the trachea, and a number of blood vessels and (2) the *pericardium*, which contains the heart.

In breathing, the capacity of the thoracic cavity is markedly changed by the movements of its walls. When the muscles of the diaphragm contract, the latter becomes much less dome-shaped, and the floor of the thorax is considerably lowered. At the same time, contraction of the intercostal muscles lifts the anterior ends of the downward sloping ribs, increasing the depth of the thorax from front to back, and rotates them slightly outward, increasing the breadth of the thorax from side to side. The space between the inner and outer pleural membranes is airtight,

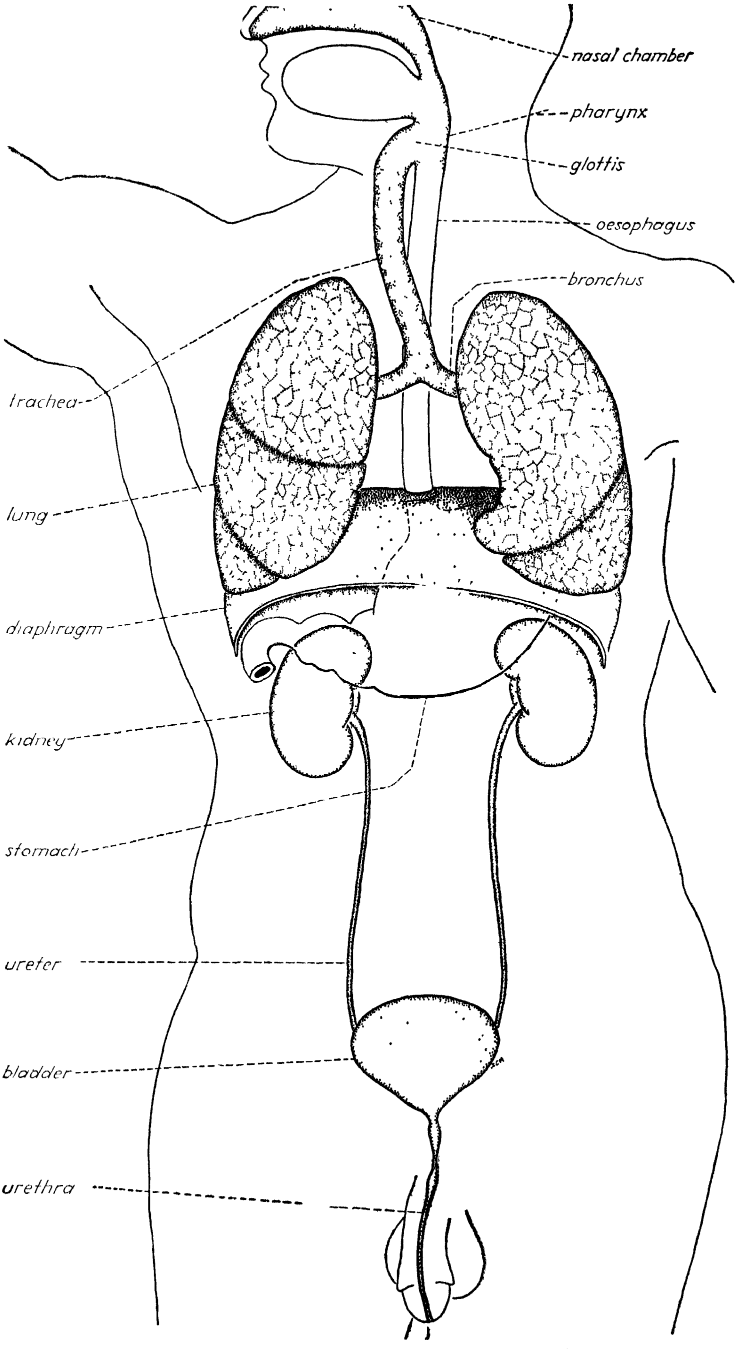
nasal chamber
pharynx
glottis
oesophagus
bronchus
trachea
lung
diaphragm
kidney
stomach
ureter
bladder
urethra

FIG. 30. *The respiratory and excretory systems superimposed upon an outline of the human body. (Modified from Clendenning and others.)*

and when the outer pleural membrane is pulled outward and downward by its tight connection to the diaphragm and body walls, the elastic inner pleural membrane must likewise expand. Since the inner pleural membrane is closely attached to the air sacs of the lungs, they too must enlarge and so draw in[1] air through the bronchial tubes, trachea, and upper air passages to fill the expanded lungs.

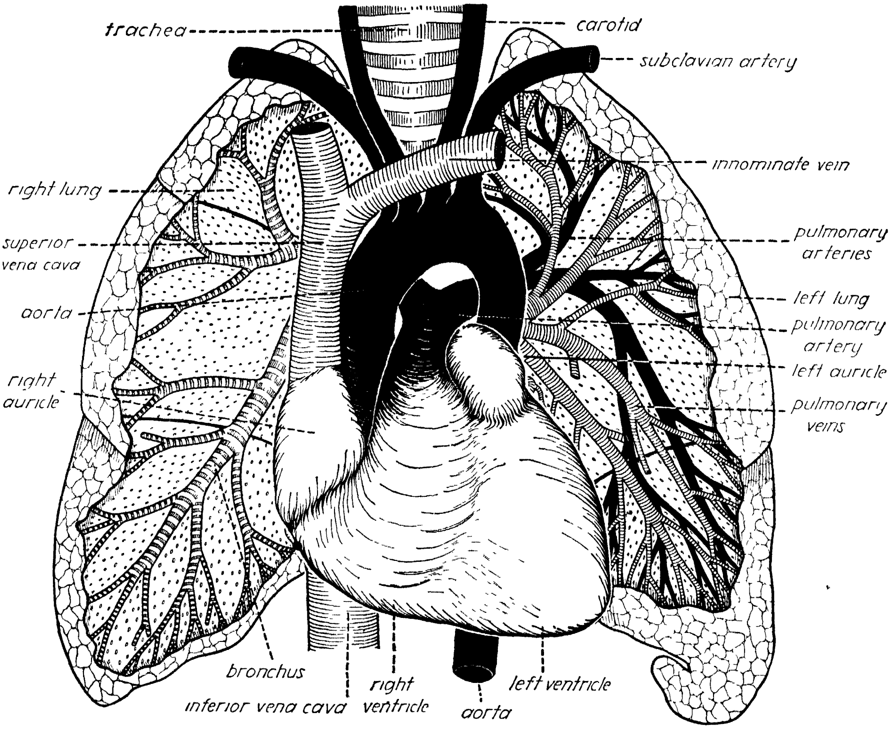
trachea
carotid
subclavian artery
innominate vein
right lung
superior vena cava
pulmonary arteries
left lung
aorta
pulmonary artery
right auricle
left auricle
pulmonary veins
bronchus
inferior vena cava
right ventricle
aorta
left ventricle

FIG. 31. *The heart and lungs in ventral view, showing the close relations that exist between them. Arteries indicated in solid black, veins shaded. The pulmonary veins and arteries are shown in the dissected lung at the right, the air tubes in the lung at the left. (Modified from Turtox Classroom Charts, courtesy of the General Biological Supply Company.)*

Relaxation of the muscles allows the lifted ribs and tightened diaphragm to return to their resting positions, and the contracting thoracic walls force the excess air from the lungs. The alternation of these opposing movements—*inspiration* when the thoracic cavity expands, *expiration* when it contracts—serves to keep the air in the lungs continually refreshed.

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[1] More accurately, since the atmosphere about us is under a pressure of nearly 15 pounds per square inch, air is forced into a region of lowered pressure.

External Respiration. The air entering the alveoli is brought into very close proximity to the blood that flows through the lungs. The lining of each alveolus consists of a single layer of flat epithelial cells, on the outer surface of which the thin-walled capillaries of the blood system form a close network. Gases readily diffuse through the alveolar epithelium and capillary walls and so can pass from a region of higher concentration to one of lower concentration. The blood entering the lungs has come from the other body tissues, where it has lost all oxygen and taken up a large amount of carbon dioxide. The air in the alveoli, on the other hand, is comparatively high in oxygen and low in carbon dioxide. Consequently oxygen passes from the alveoli into the blood and carbon dioxide from the blood into the alveoli. The fluid blood can take into solution only a small amount of oxygen, but the *hemoglobin* of the red blood cells absorbs oxygen molecules to form the loosely combined *oxyhemoglobin* that gives arterial blood its red color. Hemoglobin thus immensely increases the capacity of the blood for oxygen.[1] The gaseous interchange between the blood and the air in the lungs constitutes external respiration, as a result of which the blood that leaves the lungs is rich in oxygen and low in carbon dioxide.

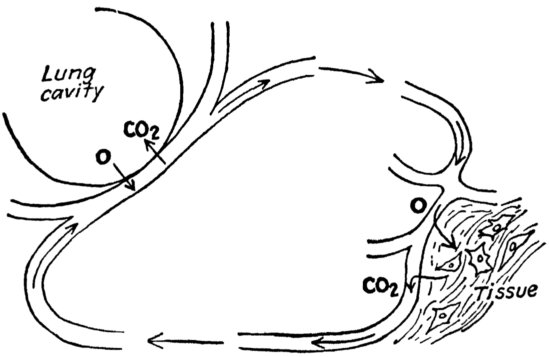

FIG. 32. *Diagram to compare internal and external respiration.* (*From* Wolcott, *Animal Biology.*)

Internal Respiration. When the blood from the lungs reaches the other body tissues, it again enters capillary vessels that permit a gaseous exchange. Here the exchange is with tissues that are poor in oxygen and have a high carbon dioxide concentration. Oxygen in the blood now diffuses out from the capillaries (the oxyhemoglobin losing its oxygen and taking on the dark red color of venous blood), and carbon dioxide diffuses into the blood. This interchange constitutes internal respiration. Here the oxygen is delivered to the ultimate consumer—the tissues—and here the carbon dioxide is taken from its original source in the body.

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[1] Hemoglobin is a protein with a molecular weight of about 68,000. Its molecule contains four smaller units of structure, each having a weight of about 17,000 and containing globin and hemin, the latter including a single atom of ferrous iron. Each iron atom is able to unite loosely with an oxygen molecule (O_2), so that in changing to oxyhemoglobin each hemoglobin molecule takes on four oxygen molecules. The reaction is freely reversible: Hemoglobin + $4O_2 \leftrightarrows$ oxyhemoglobin. Since it has been calculated that a single red corpuscle contains about 240 million hemoglobin molecules, its oxygen capacity is approximately 960 million oxygen molecules.

EXCRETION AND THE EXCRETORY SYSTEM

We have seen that the materials taken into the body through the digestive and respiratory systems are utilized for growth, repair, and the liberation of energy. These processes, however, also result in the production of waste substances that become distinctly poisonous if allowed to accumulate.

As was pointed out in the beginning of this chapter, the wastes resulting from cell metabolism (chiefly oxidation) are water, carbon dioxide, nitrogenous salts (urea), and inorganic salts. One of these, carbon dioxide, is a gas; this substance is eliminated principally through the lungs, together with water in the form of water vapor. The other products of cell metabolism are nongaseous and require a different means of elimination; it is with this group of wastes that the organs of excretion are mainly concerned. In addition to the metabolic wastes, there are other waste products of the body, such as feces and dead skin, hair, and nails. *Feces* consists of the indigestible or undigested portions of the food eaten, together with bile pigments and other products of digestive glands, and bacteria and other organisms that multiply in the intestines. This material is eliminated by the action of the large intestine. Dead portions of the skin and its appendages are mechanically shed from the body surface.

The portions of the body that function as excretory organs are not all included in the excretory system proper. They are tabulated below, together with the products that they eliminate.

Organs	*Excretory function*	*Substances eliminated*
Kidneys.	Primary	Water and soluble salts resulting from protein metabolism—chiefly nitrogenous wastes
Lungs	Secondary	Carbon dioxide and water vapor in exhaled air
Skin	Secondary	Water, carbon dioxide, and salts, as sweat
Alimentary canal. .	Secondary	Feces, bile pigments, water, and salts (chiefly nonnitrogenous)

The Excretion of Nitrogenous Wastes

Nitrogenous wastes, formed by the continual wearing out of protoplasm and from the nitrogenous portion of such amino acids as are oxidized for energy, together with certain salts and a part of the excess body water, are eliminated by a special excretory system.

The ***excretory system*** consists of a pair of kidneys; a urinary bladder; the paired tubular ureters that lead from the kidneys to the bladder; and the urethra, a tube extending from the bladder to the exterior of the body. Each *kidney* is a compact, glandular organ somewhat larger than the fist. One lies on each side of the mid-dorsal line of the abdominal cavity in the region of the small of the back. The medial (inner) margin of each kidney is concave, and on this concave side, the kidney contains a funnel-shaped space that leads into the ureter. In this same region, the kidney also receives a large artery and gives off a vein. Internally the kidney is closely packed with a multitude of microscopic tubules. Each tubule begins in an expanded and invaginated blind end (*Bowman's capsule*) situated near the outer surface of the kidney. Beyond this expanded portion, the tubule becomes truly tubular and after several

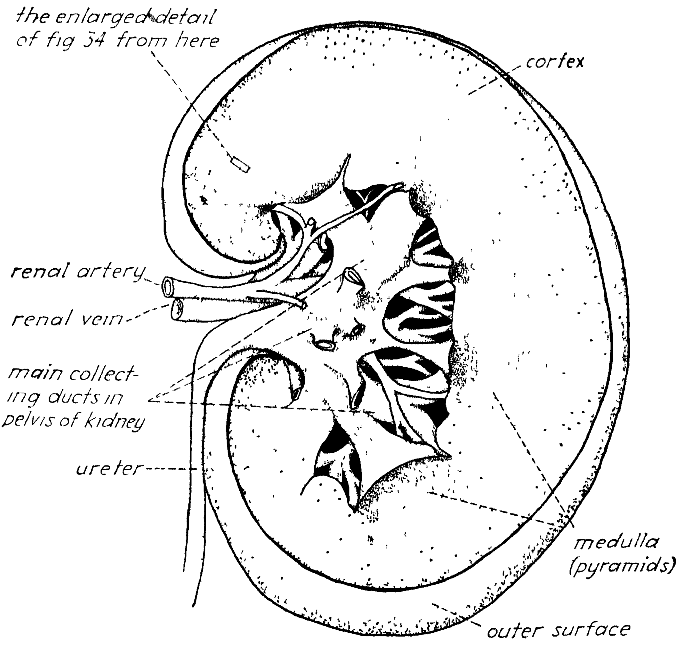
the enlarged detail of fig 34 from here
cortex
renal artery
renal vein
main collecting ducts in pelvis of kidney
ureter
medulla (pyramids)
outer surface

FIG. 33. *A longitudinal section through the kidney, showing the relations between arteries, veins, and urinary tubes. (Redrawn from Maximow, Textbook of Histology, W. B. Saunders Company.*

loops and turnings, runs into a larger collecting duct; this, in turn, leads to the funnel-shaped cavity that ends in the ureter.

Each of the millions of Bowman's capsules[1] encloses a dense network known as a *glomerulus*, a capsule and glomerulus together forming the structure known as a *Malpighian corpuscle*. Each glomerulus is supplied by a tiny artery and is drained by an even smaller vein,[2] so that the blood pressure within the capillaries of the capsule is unusually high. A somewhat more diffuse network of capillaries is also in close contact with the walls of the long tubular portion of each tubule.

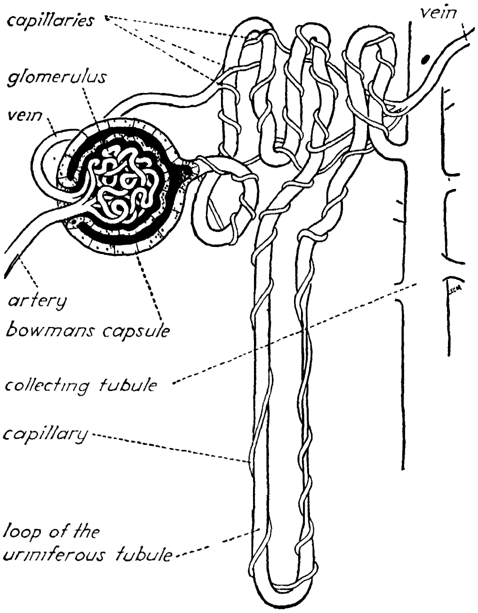

Fig. 34. *Diagrammatic figure of a Malpighian corpuscle and a uriniferous tubule. From the area of the kidney indicated in Fig. 33. (Redrawn after Amberson and Smith, Outline of Physiology, The Williams & Wilkins Company.)*

Blood, entering the glomerulus under pressure, is filtered in large quantities through the thin walls of the capillaries and the thin inner wall of the capsule into the expanded upper end of the tubule. Blood corpuscles and colloidal particles do not pass through the walls of the capillaries, but in most other respects the filtrate is little different from the plasma of the blood. This fluid, in the course of its long tortuous passage through the tubule, returns the greater portion of its water and nearly all its nonwaste materials back to the blood stream, by way of the walls of the tubule and their surrounding network of capillaries. The reduced amount of fluid that reaches the lower portion of the tubule contains the dissolved nitrogenous (and other) wastes and is known as *urine.*

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[1] There are no fewer than one million Bowman's capsules in each kidney.

[2] Elsewhere in the body, the vein that receives blood from a set of capillaries usually has a larger bore than does the artery that supplies the same capillaries.

The minute quantity of urine formed in each tubule passes into a larger collecting duct (each duct receives the discharge of many tubules); and the thousands of ducts empty into the pelvis of the kidney and thence into the *ureter,* through which the urine is propelled by muscular contractions into the *bladder.* The latter is a hollow muscular organ located in the lower, ventral part of the abdominal cavity. A tube, the *urethra,* leads from the lower, funnellike end of the bladder to an opening on the outside of the body. The juncture of the bladder and urethra is closed by a muscular valve, so that the urine that continuously flows into the bladder from the kidneys is stored in the bladder (which may become markedly distended), until a voluntary impulse causes the muscular valve to relax. Contraction of the muscular wall of the bladder then expels the urine from the body.

Although not ordinarily considered a part of the excretory system, the *liver* also plays a role in the excretion of nitrogenous wastes. It removes a considerable variety of waste nitrogenous compounds from the blood, transforms them into urea, and returns the urea to the blood, to be carried to the kidneys. It also takes from the blood certain waste products formed by the breakdown of hemoglobin and excretes them in the bile in the form of bile pigments. The *skin* has a minor excretory function in its elimination of part of the excess body water and certain salts through the sweat glands.

CHAPTER VI

The Circulatory System: The Common Carrier for the Body

Although the circulatory system might logically be classed, along with the nervous and endocrine systems, among the coordinating systems of the body, its role as a coordinator is the result of the fact that it acts as the common carrier for all of the other body parts. As a transport system, it is intimately involved in the functioning of all the other systems, providing for a rapid collection from and delivery to all the tissues of the body. Its chief functions may be listed as follows:

1. It carries digested food from the intestine (and liver) to all tissues.
2. It carries oxygen from the lungs to the tissues and carbon dioxide from the tissues to the lungs.
3. It carries nitrogenous wastes from the tissues to the kidneys.
4. It connects the heat-producing tissues (chiefly muscles) and the heat-eliminating skin (and lungs) with the rest of the body and so maintains a fairly uniform temperature throughout the body.
5. It carries hormones (chemical messengers) from the glands where they are produced to the regions of the body where they regulate activity.
6. It acts as a defense mechanism against disease-producing organisms by
    - *a.* Producing antitoxins and antibodies.
    - *b.* Producing white blood cells and transporting them to the invaded region, where they attack and engulf certain types of disease-producing organisms.
7. It protects its own system from loss of blood by forming clots in cut or broken vessels.

Essentially the circulatory system comprises a circulating fluid (the *blood*), a muscular pump (the *heart*), an intricate system of pipe lines (*arteries*, *veins*, and *capillaries*) that carry the blood from the heart to all parts of the body and back to the heart, and accessory drainage tubes (the *lymphatics*) that collect the leakage from the blood pipe lines and return it to the main circulation.

Blood is a tissue consisting of a fluid, noncellular portion and a tremendous number of blood cells of various types (the *corpuscles*). It makes up about 5 per cent of the entire body weight, so that in a man weighing 150 pounds there should be 7½ pounds of blood, or approximately 7½ pints. Somewhat more than half of this volume is made up of the fluid portion, or *plasma*, which consists of about 90 per cent water and 10 per cent of a complex and somewhat variable mixture of proteins, carbohydrates, fats, various salts, nitrogenous wastes, internal secretions, and the substances that make possible the individual's immunity to certain diseases.

The *blood cells*, or corpuscles, are of three principal types: red blood cells, white blood cells, and the blood platelets (Fig. 6).

The *red blood cells* are the most numerous and give blood its red color. Each is a biconcave disk about eight-thousandths of a millimeter in diameter, and there are about 6 million red blood cells to each cubic millimeter of blood. These cells are peculiar in lacking nuclei. Their red color is due to the hemoglobin that they contain, and their function, as we saw in the account of the respiratory system, is to carry oxygen from the lungs to the tissues and, to a less marked extent, to carry carbon dioxide from the tissues to the lungs.

The *white blood cells* are of several types, which may be grouped as granular and nongranular; all contain nuclei. They are much less numerous than the red blood cells, averaging perhaps 5,000 per cubic millimeter in the normal individual, but are capable, under certain conditions of infection (appendicitis, for instance), of multiplying until there may be as many as 30,000 per cubic millimeter. The functions of the white blood cells are various. Certain types play an important part in defending the body against the invasion of disease-producing organisms, and others are important in the healing of wounds.

The *platelets* are biconvex disks somewhat less than half the diameter of the red blood cells. They are of importance in the complex process of forming blood clots, described below.

Blood-cell Formation. Red blood cells live for only a short time, estimated at 15 to 40 days. The life span of white blood cells is even shorter, perhaps less than 3 days. Both must, therefore, be continuously replenished. This is accomplished by the so-called "blood-forming organs." The primary source of the nongranular white cells is lymphoid tissue, found in the lymph nodes, tonsils, and spleen. The red blood cells and the granular white cells are formed in the red bone marrow (and perhaps the lungs). The regions of most active red-cell formation are the vertebrae, ribs, sternum, proximal ends of the humerus and femur, and portions of the cranial bones. The red blood cells are nucleated to begin with but lose their nuclei before they enter the blood.

The *spleen* is one of the organs associated with blood-cell formation, but its functions are not completely understood. It is an ovoid body about 5 inches long, weighing about 6 ounces, located in the upper left portion of the abdominal cavity. This organ is composed of several kinds of tissue, and many different functions have been assigned to it. It contains a reserve supply of blood and is capable of some contraction, thus perhaps aiding in the regulation of the volume of blood in the vessels of the circulatory system. It probably aids in the destruction of old or dead blood cells and is known to be a source of new nongranular white blood cells.

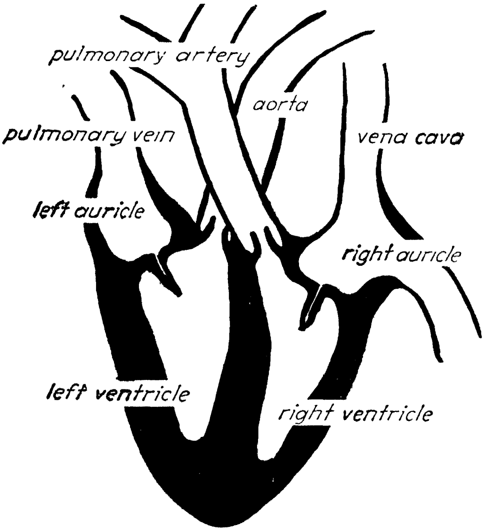

FIG. 35. *Dorsal view of the heart, showing its four chambers, and the arteries, veins, and heart valves diagrammatically. In this drawing the ventricles are shown just beginning to contract. Their contraction forces open the valves of the arteries and closes the auricular-ventricular valves. (From Carlson and Johnson, The Machinery of the Body, The University of Chicago Press.)*

The heart is a powerful muscular organ situated nearly in the center of the lower part of the thoracic cavity. It is enclosed in a tough membranous sac, the *pericardium*, which contains the pericardial fluid that bathes the heart and protects it from friction with the surrounding organs. The heart is divided into four chambers. The upper two are the relatively thin-walled *auricles*, which receive the blood that is returned to the heart from the veins. The two lower chambers, the *ventricles*, have heavy muscular walls that, by contracting, propel the blood throughout the body. The auricle and ventricle on the same side of the heart are connected by a valve that permits the blood from the auricle to pass into the ventricle; but the right auricle and ventricle are completely separated from the left auricle and ventricle by strong, impervious partitions. The heart may therefore be thought of as composed of two separate pumps, often designated the *right heart* and the *left heart.*

The walls of the heart, except for thin outer and inner epithelial linings (the inner lining called *endothelium*) and some connective tissue, are composed of a special type of contractile tissue known as *cardiac* or *heart muscle.* The heart is a modified blood vessel, and its muscle tissue has the same origin as the smooth muscle of artery and vein walls; but its fibers are nevertheless cross-striated, though imperfectly so, and in this respect suggest the structure of skeletal muscle. Cardiac muscle also resembles skeletal muscle in the strength and rapidity of its contractions, but with one very important difference. A skeletal muscle is capable of graded contractions, the strength of which is dependent upon the intensity of the nerve stimulus and the resultant variation in the *number of individual muscle fibers* stimulated to contract. In the heart, on the other hand, any stimulus strong enough to cause the heart muscle to react at all will cause complete contraction of an entire auricle or ventricle. The heart chambers, as units, follow the all-or-none-rule, whereas in skeletal muscle, it is only the individual muscle fibers that behave in this way. The reason for the difference is that in skeletal muscle, the fibers are separate, whereas in cardiac muscle, they branch and join together in such a way that a stimulus spreads from fiber to fiber throughout the whole auricle or ventricle.

In a sense, the beating of the heart is automatic—*i.e.*, it is not dependent upon stimuli from the central nervous system. The heart will continue to beat if all its nerves are severed. Furthermore, on account of its all-or-none character, the contraction of any chamber of the heart is always equally strong under a given set of conditions. This does not mean that the strength of the heartbeat does not vary; as everyone knows, the state of mind or body can modify both the rate and the power of the beat. The controlling mechanisms responsible for these changes are discussed below in connection with the mechanics of circulation.

The heart muscle keeps up a rhythmic series of contractions throughout the life of the individual. Each wave of contraction begins at the upper end of the auricles, forces the blood from them into the ventricles, and then continues, more powerfully, into the walls of the ventricles. The valves between the auricles and ventricles permit blood to flow into the ventricles but prevent its being forced back into the auricles when the ventricles contract. Instead, the blood from the left ventricle is forced into the main systemic artery, the *aorta;* that from the right ventricle, into the *pulmonary artery* leading to the lungs.

Blood vessels are of three main types: *arteries,* which carry blood from the heart to the tissues; *veins,* which carry blood from the tissues to the heart; and *capillaries,* the minute blood vessels in the tissues that connect the arteries with the veins. The walls of the arteries and veins have much the same structure, but the walls of the arteries are markedly heavier and stronger than the walls of the veins. In both, a smooth, thin lining of epithelial cells (endothelium) is surrounded by several layers of smooth muscle cells and connective tissue. The walls of the capillaries lack the smooth muscle and connective tissue layers and consist of a single layer of thin endothelial cells.

The great arteries that leave the heart, the *aorta* and *pulmonary artery,* branch into successively smaller ones, so that all parts of the body are supplied with an abundance of small arteries. These continue to branch until they pass into the enormous network of capillaries. The latter, after a short course through the tissues, unite to form small veinlets. These, in turn, unite to form larger and larger veins and finally pour their blood into the great veins that lead back to the heart—the *pulmonary veins* from the lungs, entering the left auricle, and the two *venae cavae,* entering the right auricle. The veins of the lower part of the body empty into the *inferior vena cava,* those of the head, neck, and arms into the *superior vena cava.*

The capillaries have the task of bringing the blood into the immediate vicinity of the cells, and it is essential that no cell be far removed from a capillary. For this condition to exist it is necessary that the capillaries be exceedingly numerous. It has been calculated that the capillaries in the human body, if placed end to end, would form a tube 62,000 miles long. Since each capillary is only about a millimeter in length, the number of capillaries is beyond comprehension. To illustrate the closeness of the spacing of cells and capillaries, it may be noted that there are about 2,500 capillaries in a cross section of 1 sq. mm. of skeletal muscle, or about 1,562,500 per square inch. The total surface of the 62,000-mile capillary tube mentioned above is about 67,000 square feet, or 1½ acres; and it has been calculated that 1 cc. of blood is exposed to a capillary surface of 7,300 sq. mm., or 8 square feet. The cross-sectional area of the total capillary network is estimated as 400 to 1,000 times that of the aorta, and considering the relatively small amount of blood in the entire vascular system, it is evident that all these capillaries cannot be filled at the same time. As is mentioned below in connection with the lymphatic system, only a part of the capillaries of a resting organ contain blood at any one time, but the entire capillary system of the organ may become filled during periods of activity.

FUNCTIONAL DIVISIONS OF THE CIRCULATORY SYSTEM

The Pulmonary Circulation. In man, as in all the higher vertebrates, the circulatory system is double. The *right* auricle and ventricle receive only the dark venous blood that has returned to the heart from all the tissues of the body except the lungs. When the heart contracts, the blood from the right ventricle is forced into the pulmonary artery, which leads to the lungs. In the lungs, the blood enters the capillaries that are in contact with the alveoli, loses its load of carbon dioxide, and becomes oxygenated. The capillaries of the lungs lead to veins that unite to form the large pulmonary veins. These lead back to the heart and empty into the *left* auricle.

The Systemic Circulation. The blood that returns to the *left* side of the heart from the pulmonary circulation is the bright-red oxygenated blood that is often termed *arterial blood.* Contractions of the left ventricle force it out into the *aorta,* the largest artery of the body, which sends branches to all parts of the body except the lungs. The capillaries supplied from the systemic arteries bring arterial blood into intimate contact with the tissues. Blood leaving the capillaries passes into the veins, and the two venae cavae finally return the now deoxygenated dark-red venous blood to the *right* auricle, from which it will be taken into the pulmonary circulation.

The routes that the blood may traverse in the systemic circulation are varied, but except for a considerable portion carried to the digestive system, the blood from each region returns directly to the heart after traversing a single set of capillaries.

The Portal System. Certain of the large abdominal arteries that lead from the aorta carry blood to the stomach, intestines, liver, pancreas, and spleen. Here the blood supplies the needed oxygen and takes up the excess carbon dioxide and nitrogenous wastes and also the digested foods that have passed through the walls of the intestine. From the capillaries of these organs, this blood passes finally into a large vein, the *hepatic portal,* which carries the blood to the liver, where it enters a second set of capillaries that form a network in the tissues of the liver.[1] From the capillaries of the liver, the blood again passes into a venous system, which leads to the heart.

The Lymphatic System. Although all the materials used by the cells of the body are obtained from the blood and all the waste products of cell metabolism find their way into it, blood as such does not come into direct contact with the cells. It remains within the capillaries and these capillaries in most instances are not even in immediate contact with

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[1] In the liver, the surplus monosaccharides are taken from the blood and stored in the liver cells.

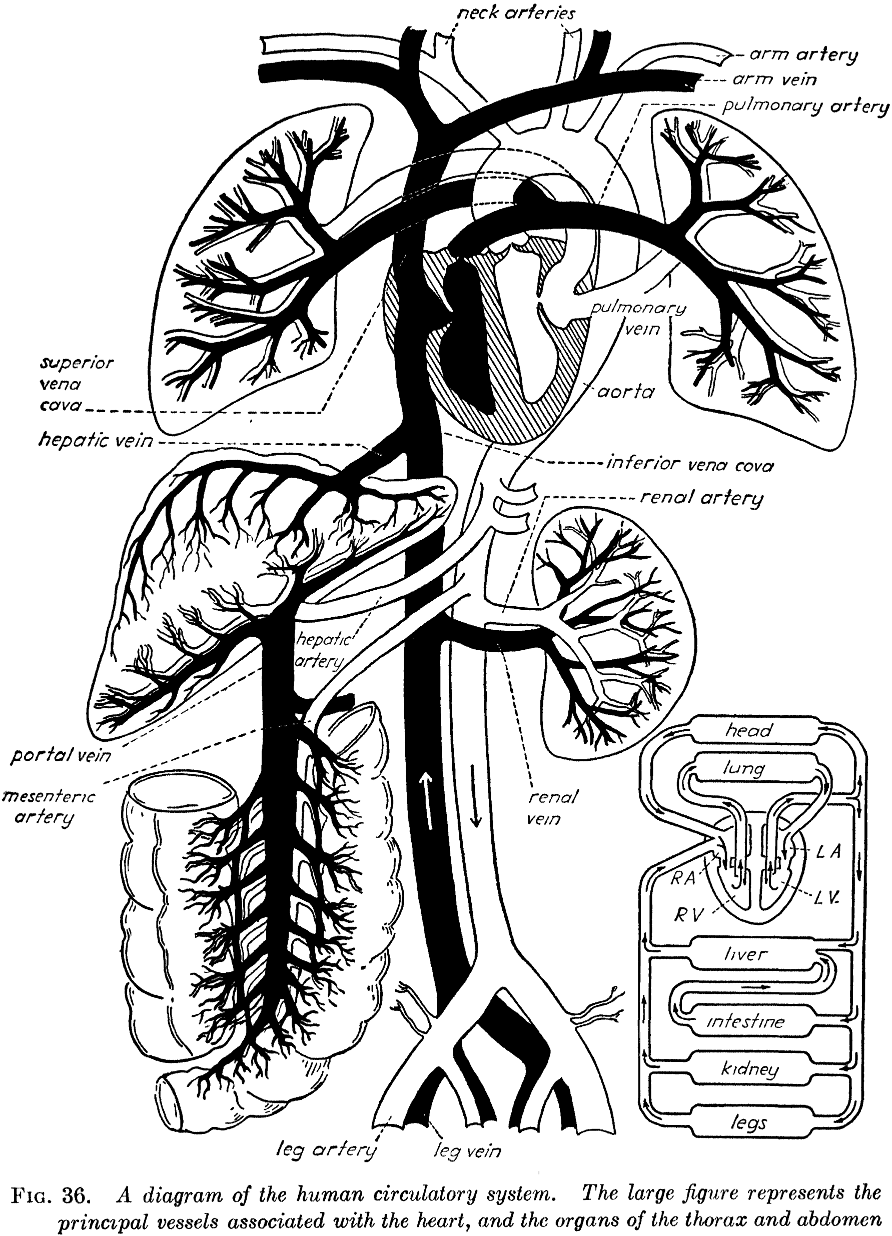
neck arteries
arm artery
arm vein
pulmonary artery
superior vena cava
pulmonary vein
aorta
hepatic vein
inferior vena cava
renal artery
hepatic artery
portal vein
mesenteric artery
renal vein
leg artery
leg vein
head
lung
LA
RA
LV.
RV
liver
intestine
kidney
legs

FIG. 36. *A diagram of the human circulatory system. The large figure represents the principal vessels associated with the heart, and the organs of the thorax and abdomen which they supply. The solid black vessels (both veins and arteries) are carrying blood low in oxygen pressure and high in carbon dioxide, the white vessels (veins and arteries) are carrying blood high in oxygen and low in carbon dioxide. The inset in the lower right-hand corner diagrammatically shows the direction of the flow of blood throughout this system. (Modified, by permission, from Girard,* The Body Functions, *John Wiley & Sons, Inc.)*

the cells. Between the capillaries and the cells, and between the cells, there exists a multitude of *tissue* or *lymph spaces*, mostly microscopically small but varying much in size and shape. Filling these spaces and bathing the cells is a tissue fluid, the *lymph.*[1] Lymph is formed by a "leakage" of water, salts, glucose, amino acids, etc., from the blood capillaries into the surrounding tissue spaces. The red blood cells do not pass through the capillary walls; but many of the white blood cells force their way, amoeba-like, between the endothelial cells composing these walls and enter the lymph spaces. Although the tissue fluid at first probably differs little from blood plasma, it is soon modified by the activities of the cells with which it is in contact; they take from the lymph the food substances that they need, and discharge into it their waste products. Being constantly bathed by the tissue fluid, the cells of the body may truthfully be said to be aquatic, the tissue fluid constituting their environment or internal medium.

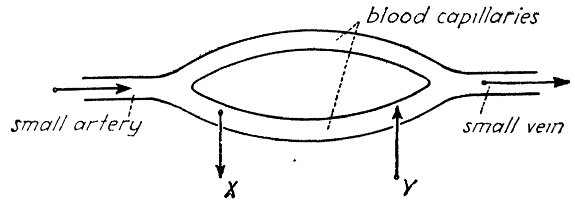

FIG. 37. *Diagram to show pressure relationships concerned in the loss and recovery of fluid from the capillaries. At X the hydrostatic blood pressure within the capillaries exceeds the combined osmotic pressure of the blood and lymph pressure outside the capillaries, causing fluid to escape. At Y the pressure relationships are reversed, causing fluid to re-enter the capillary.*

It is evident that there must be some means of preventing stagnation of the lymph in the tissue spaces—of draining off the "used" lymph, waste-charged and low in food, and of replacing it with fresh lymph. There are two mechanisms by which this is accomplished—the lymphatic system, discussed below, and the blood capillaries themselves. It may seem paradoxical that the same capillaries that lose fluid to the tissue spaces to form lymph should also absorb "used" lymph back into the blood stream; but this can be understood in the light of the following considerations (see Fig. 37).

The chief factor in forcing the fluid of the blood into the tissue spaces is the hydrostatic blood pressure in the capillaries, produced by the beating of the heart. Were this not opposed by the osmotic pressure of the blood caused by its contained colloidal proteins, and by the pressure of the lymph already in the tissue spaces, most or all of the blood fluid would be forced out through the walls of the capillaries. As it is, wherever the hydrostatic blood pressure exceeds the combined effects of the osmotic and lymph pressures, fluid does escape from the capillaries; where the forces are balanced, there is no loss or gain of fluid; and where the osmotic pressure plus the lymph pressure exceeds the hydrostatic blood pressure, fluid enters the capillaries. Hydrostatic blood pressure is high near the arterial ends of the capillaries (at X in Fig. 37), and here fluid is lost. However, the hydrostatic pressure falls rapidly along the course of each capillary, because of friction and loss of fluid, and the colloidal proteins become more concentrated, causing an increase in osmotic pressure within the capillary. As a consequence, the pressure relations are reversed toward the venous ends of the capillaries (at Y in Fig. 37), and here lymph tends to flow back through the capillary wall into the blood stream.

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[1] A distinction is sometimes made between tissue fluid and lymph, the latter term being then restricted to the fluid contained within the lymph vessels.

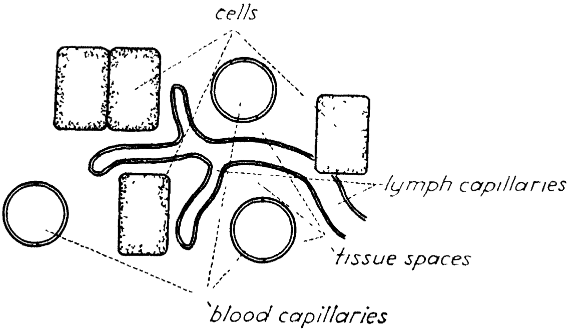

FIG. 38. *Diagram to show the relationships between the blood capillaries, tissue spaces, cells, and lymph capillaries in a tissue. The blood capillaries are shown in cross section, the lymph capillaries in longitudinal section* (*Redrawn from Zoethout and Tuttle, Textbook of Physiology, The C. V. Mosby Company.*)

Diffusion also plays an important part in the blood-lymph relations. Blood entering the capillaries is rich in oxygen and dissolved foods and low in metabolic wastes. Lymph is low in food and oxygen, which are continually removed from it by the cells, and is high in wastes received from the cells. It results that oxygen and food substances continually diffuse through the capillary walls into the lymph, and wastes diffuse in the opposite direction into the blood. Of all the food substances, the colloidal proteins pass through the capillary walls with the greatest difficulty, their concentration being therefore always much greater in the blood than in the lymph.

During the inactive state of an organ, nearly all the lymph is drained directly into the blood capillaries; but increased activity of the organ brings greater blood supply and increases the formation of lymph. This is partly the result of increased blood pressure but is more largely caused by a great increase in the capillary surface. As was mentioned above, only a fraction of the capillaries of a resting organ contain blood, the remainder being collapsed and empty. In a resting muscle, for example, a cross section of 1 sq. mm. of muscle tissue shows only about 200 open capillaries. When the muscle becomes active, however, a combination of nervous and chemical stimuli causes the small arteries and capillaries to dilate, enormously increasing the blood flow through the organ. In a cross section of 1 sq. mm. of active muscle, there are about 2,500 open capillaries—more than twelve times as many as in the resting muscle.

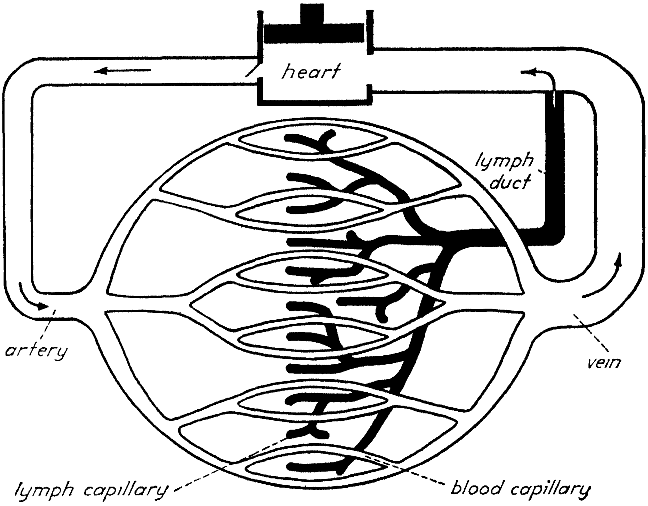

FIG. 39. *Relationship of the lymphatic system (shown in black) and the blood circulatory system. The direction of the flow of blood and lymph is indicated by the arrows. (From Carlson and Johnson, The Machinery of the Body, The University of Chicago Press.)*

Each capillary is furthermore dilated, offering more surface for filtration of lymph into the tissue spaces. With the increase in leakage, the capillaries can no longer absorb the lymph as rapidly as it forms, and the lymphatic system comes into operation.

The lymphatic system is an accessory circulatory or drainage system. Like the blood circulatory system, it is made up of tubes, in this case called *lymph vessels;* but unlike that system, it does not form a continuous closed circuit but is a many-branched one-way drainage system comparable to a river with its affluents and head waters. It contains no pumping organ and has nothing analogous to the arteries; but it may be likened to the capillary and vein portions of the blood circulatory system. In all the tissue spaces, there are very delicate tubes, the lymph capillaries (Fig. 38), closed at the ends but communicating freely with each other and fusing to form larger and larger vessels. The latter resemble veins and, like them, are provided with valves that permit the movement of lymph only in one direction, toward the heart. The large lymph vessels finally converge to the region of the left shoulder, where the main *thoracic duct* empties the lymph into a large vein of the blood circulatory system. This duct carries the lymph from all parts of the body except the right side of the head, neck, and thorax and the right arm; the lymph from those regions enters the corresponding vein on the right side of the body. Movement of the lymph in the vessels is brought about by muscular movements of the body that incidentally compress the lymph vessels and squeeze the lymph in the direction determined by the valves.

The intimate contact between the lymph and the tissue cells supplements and completes the functioning of the circulatory system proper by permitting a much more complete interchange between the circulating medium and the body tissues. The lymphatic system also provides an important means of defense against the invasion of the body by disease-producing organisms. Most of the lymph vessels have, at intervals, small filterlike enlargements, the *lymph nodes,* where numerous white blood cells collect. Here invading bacteria, as well as worn-out cell fragments, are ordinarily destroyed by the white blood cells before they can be carried into the blood stream.

THE MECHANICS OF CIRCULATION

We have seen that it is the powerful contraction of the ventricles that pumps the blood out along the arteries. When the ventricles contract, 50 to 100 cc. of blood is forced into the aorta and an equal amount into the pulmonary artery. The passage of the blood through the smaller arteries, especially through the fine capillaries, encounters marked frictional resistance, so that the blood in the arteries is always under pressure, which somewhat distends the elastic walls of these vessels. The elasticity of the arteries continues to force the blood into the capillaries, even in the intervals between heartbeats. Each beat of the heart suddenly pumps another 50 to 100 cc. of blood into the aorta and pulmonary artery, and the increased pressure causes a short section of the elastic artery walls to expand. The wave of pressure travels rapidly out over the arteries and their branches at a rate 10 to 15 times as fast as the flow of the blood itself and is gradually extinguished in the smaller arteries. It is the succession of such impulses, or pressure waves, produced by the rhythmic contractions of the ventricles and accompanied by a bulging of the arterial wall, that constitutes the *pulse,* by means of which the rate of heartbeat can be determined. It is also this series of repeated impulses from the heart that produces an alternating maximal (*systolic*) and minimal (*diastolic*) pressure in the arteries.[1]

Owing to the damping out of the pulse, by friction and the elasticity of the arterial walls, blood enters the capillaries in an almost steady stream. The capillary resistance to flow is so great that nearly all the pressure created by the beating of the heart is utilized in overcoming it; only a small residue of this pressure remains when the blood flows from the capillaries into the veins. The return of the blood to the heart is caused, in part, by this residual pressure but is greatly aided by other factors. We have already noted that the veins, like the lymphatics, are well provided with valves opening in the direction of the heart. Muscular movements of the body, including movements of the viscera and those of breathing, aid in the return flow by squeezing the veins and forcing the blood in the direction determined by the valves. The breathing movements also assist the process in another manner. The same movements of the diaphragm and ribs that reduce the pressure within the thoracic cavity, causing air to flow into the lungs, also reduce the pressure in the auricles and the veins that lie within this cavity and tend to "pull" blood into the auricles and adjacent portions of the venae cavae.

In response to variations in the circulatory needs of the body, the normal heart is capable of making great adjustments in rate and *power* of beat and in the volume of blood discharged at each stroke. While the body is at rest, the amount of blood discharged from each ventricle averages about 50 cc. per stroke; at maximum capacity, the heart can increase this amount to about 150 or 200 cc. per stroke. This is not, as might be thought, a contradiction of the all-or-none principle already described as governing the contraction of the heart. Under a given set of conditions, it remains true that each beat of the heart is as strong as every other beat and that the strength of the beat is independent of the strength of the stimulus. But in heart muscle, as in skeletal muscle, the muscle fibers (within limits) contract the more powerfully the more they are stretched when contraction begins. If for any cause the volume of blood entering the auricles is increased, this stretches the heart muscles, and the resulting contraction is more powerful and expels a greater volume of blood. Increased muscular activity, accompanied by more rapid and powerful respiratory movements, is one of the more common conditions that will cause an increased flow of venous blood into the heart, automatically bringing about an increase in the strength of the heart contraction.

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[1] The average normal blood pressure increases slowly with age; this is often attributed to the loss of elasticity and tone of the arteries, but its cause is somewhat obscure. Average values of systolic and diastolic pressures at various ages, in terms of millimeters of mercury, are as follows:

Age in years	10	20	30	50	60
Systolic pressure	103	120	123	130	135
Diastolic pressure	70	80	82	86	89

The mechanism controlling the *rate* of heartbeat is quite complex, involving physical, chemical, and nervous stimuli.[1] We shall be able only briefly to consider some of the factors involved. First of all, we may recall our earlier statement that the beating of the heart is "automatic," produced by an "inner stimulus," and that it goes on even in the absence of outside stimulation. The heart is, however, subject to influences that modify its independent activity. It is connected with the central nervous system by two nerves[2]—the *vagus* and the *cervical sympathetic.* Cutting these nerves does not stop the action of the heart; their function is merely regulatory. Impulses from the vagus slow the heartbeat or, if sufficiently intense, may cause it temporarily to cease.[3] Impulses from the cervical sympathetic nerve accelerate its rate. Both these nerves possess "tone"; *i.e.*, they both transmit impulses more or less continuously, and the rate of the heartbeat is in large part a resultant of the balance between the stimuli received from the two nerves. The vagus may be thought of as the "brake" upon heart action; the cervical sympathetic nerve, as the "accelerator." Increase in the inhibitory impulses from the vagus may be brought about reflexly by stimulation of certain sensory nerves, including those of the viscera, skin, and sense organs. In this connection, the sensory nerves of the aorta, the venae cavae, and right auricle are of particular importance. For instance, sensory stimuli caused by increase of blood pressure in the aorta affect the vagus, slowing the heartbeat and thus automatically lowering the pressure and safeguarding the heart and arteries against excessive strain.

Heartbeat rate commonly varies inversely as the blood pressure, although since the controlling factors are numerous and are not the same for the two phenomena, the relation is naturally not a fixed one. As an illustration of a case in which this relationship does hold, the heartbeat is rapid immediately following a severe hemorrhage, when blood pressure is very low. In this condition, no great force of heartbeat is possible or necessary, the heart chambers not being much distended; but the small amount of blood left in the vessels must be distributed as quickly and used as often as possible.

The emotions also have a pronounced effect upon the heart. Strong emotion, by stimulating the vagus, may slow the heart sufficiently to cause fainting. Another factor influencing the rate and power of the heartbeat is the presence of varying amounts of chemical substances in the blood. Thus increase in carbon dioxide and lactic acid concentration in the blood, as a result of muscular activity, tends to dilate the arteries and capillaries and by thus causing an increased flow of blood back to the heart affects the rate and power of its beat. One of the most important chemical effects is that produced by the hormone *adrenalin,* a substance produced by the adrenal glands and discussed more fully in the later section on the endocrine glands. This substance causes a rise in blood pressure, accompanied by strengthening of the heartbeat. In the absence of nervous control, it also increases the rate of heartbeat, but when the nerves are intact, a reflex inhibition slows the heartbeat rate and thus prevents the blood pressure from rising too high. Adrenalin also has numerous other effects on the circulatory system, including constriction of the arteries and capillaries of the skin and viscera and dilation of those of the heart and skeletal muscles.

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[1] The pulse rate is generally more rapid (1) in the female than in the male; (2) during and immediately after muscular activity; (3) during digestion or mental excitement; and (4) after sudden changes in position. The rate also changes with age; at birth it may be 130 to 150 beats per minute; in adult life it averages about 72 per minute; and in old age it falls to about 67 per minute.

[2] Actually, a right and left vagus nerve and a right and left set of cervical sympathetic nerves.

[3] Under exceptional circumstances, vagal stimulation may cause death from cessation of circulation; but normally, after a certain period of inhibition, the heart escapes from the control of the vagus and resumes its beat.

The efficiency of the heart as a pumping organ is strikingly shown by the rapidity with which the blood is circulated. According to Best and Taylor, the time required for a given blood corpuscle to make the pulmonary circuit (heart to lungs and back to heart) averages about 11 seconds in man. The length of the different systemic circuits varies so much that the time spent in traversing this part of the system cannot be accurately stated. It takes about 4 seconds for the blood to go from the heart to the capillaries of the forearm and about 6.6 seconds to return to the heart. It is calculated that the time required for the complete double circuit, from the right side of the heart to the lungs, back to the left side of the heart, out to the systemic capillaries, and back once more to the heart, probably averages 25 or 30 seconds. Blood going to the foot would, of course, take much longer than this to complete its circuit. The amount of blood pumped by the heart is also of interest. For a heart with a stroke volume of 75 cc., a rate of 70 beats per minute, and a total volume of blood in the body of 5,000 cc., a volume of blood equal to all that contained in the body will pass through a single chamber of the heart in a little less than 1 minute.[1] This does not mean, of course, that all the blood will have traversed this chamber of the heart in this time; part of the blood, on the shorter circuits, will have been through more than once, and part will not yet have passed through. The time required to handle this quantity of blood is much reduced when, as a result of exercise or other factors, the heartbeat rate and the volume discharged at each beat are increased.

THE CLOTTING OF THE BLOOD

As long as the circulatory system is uninjured, the blood is a fluid that flows freely through even the smallest capillaries. If any blood vessel is cut or ruptured, however, the escaping blood quickly clots, thus plugging the opened vessel and preventing continued bleeding. Clotting may also take place within the vessels under exceptional circumstances, especially at the site of bacterial or mechanical injury to the smooth inner wall.

In spite of familiarity with clotting and the fact that it is a constant property of all normal blood, the physicochemical mechanism responsible for it is only partially understood. Nevertheless, some of the essential steps in the process have been discovered, and consideration of these will emphasize two important points: (1) the number of delicately and precisely adjusted reactions that may be involved in an apparently simple physiological process; and (2) how much has been learned and yet how far we still are from a complete understanding of the workings of the individual organism.

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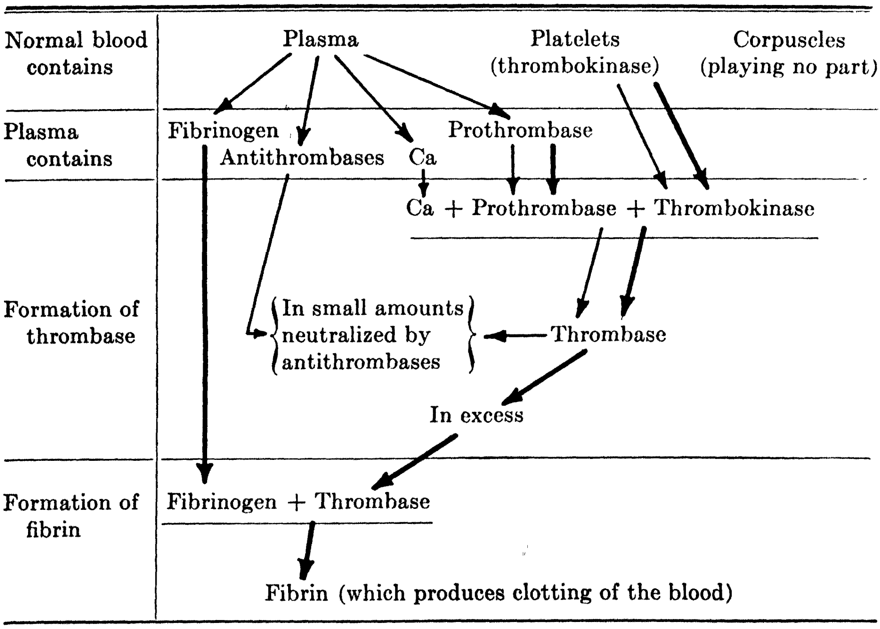
[1] 70 × 75 cc. = 5,250 cc.

When a thin film of blood is watched under the microscope while it coagulates, delicate threadlike strands can be seen to form within it. In larger quantities of blood, a dense meshwork of such strands or fibrils develops, entangling the blood cells, enclosing the liquid part of the blood, and transforming the whole mass into a sticky, jellylike substance. Contraction of the network soon takes place, squeezing out of the clot a clear yellowish fluid known as *serum*.[1] The fibrils of the network are made up of needlelike crystals of an insoluble protein called *fibrin*, and this substance is found to come from *fibrinogen*, one of the soluble proteins always present in normal blood plasma. Clotting, then, results from the change of fibrinogen to fibrin What causes this to happen when blood is shed and not within the blood vessels?

In the light of our present knowledge, the steps in this transformation seem to be approximately as follows.[2] Fibrinogen is known to be changed into fibrin by an enzyme, *thrombase;* but thrombase is not normally present in blood. Instead, it is represented in the plasma by an inactive precursor, *prothrombase*, which can be changed into the active thrombase by another enzyme, *thrombokinase*. The latter enzyme is the trigger that sets off the chain of reactions leading to clotting. Thrombokinase is not normally present in plasma, but it occurs in most cells, especially in the blood platelets, already mentioned. Breakdown of the platelets, under conditions presently to be described, liberates the enzyme into the plasma, where it reacts with the prothrombase, producing thrombase. This reaction is greatly accelerated by


Normal blood contains
Plasma
Platelets (thrombokinase)
Corpuscles (playing no part)
Plasma contains
Fibrinogen
Antithrombases
Ca
Prothrombase
Ca + Prothrombase + Thrombokinase
Formation of thrombase
In small amounts neutralized by antithrombases
Thrombase
In excess
Formation of fibrin
Fibrinogen + Thrombase
Fibrin (which produces clotting of the blood)

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[1] The main difference between serum and plasma is that the former does not contain fibrinogen and is no longer capable of clotting.

[2] It is necessary to modify the widely accepted hypothesis developed by Howell to explain clotting, in the light of more recent investigations. Other interpretations of the data than that here presented are possible.

various synapses to produce appropriate responses without our ever becoming aware of them. Some of these "routings" are permanently below the level of consciousness and cannot produce a sensory impression; others we may "by taking thought" become aware of, although we do not ordinarily sense them—as, for example, the position of a hand or foot that is quietly at rest. Any impulse that we can sense must have reached the cortex, but probably only a small proportion of even these impulses are ordinarily "conscious."

CHAPTER VIII

Coordination and Control: The Endocrine Glands

In the preceding chapter, we examined one of the two chief coordinating mechanisms of the human body—the nervous system. The other is a system of chemical coordination that depends for its functioning upon the circulatory system. The agents are a group of substances known as *hormones,* or chemical messengers– special protein substances that, transported in the blood stream to all parts of the body, stimulate appropriate reactions in particular parts of the body. A rather large number of these hormones have been discovered. The glands that produce them are peculiar in lacking ducts; their secretions enter directly into the blood that flows through the glands. Such glands are consequently known as *endocrine glands* (Greek, *endon,* "within" + *krino,* "separate"), or glands of internal secretion.

A good illustration of hormone action is furnished by *secretin,* which, as we have seen in Chap. IV, is formed by the mucosa cells of the duodenum and, when liberated into the capillaries of the intestinal wall, is carried throughout the body in the blood stream. Secretin appears to have no effect on most of the body; but when it reaches the capillaries of the pancreas, liver, and gall bladder and the enzyme-producing cells of the mucosa of the small intestine, it stimulates them to immediate activity. The pancreas pours its secretion into the intestine; the liver and gall bladder discharge bile; and the enzyme-producing cells in the intestinal wall begin to liberate their products.

Bayliss and Starling, who discovered the existence and function of secretin in 1902, demonstrated that when the acid chyme from the stomach enters the duodenum, it releases secretin from the mucosa cells into the blood stream. They had found that the intestine, liver, and pancreas continued to function when food entered the intestine from the stomach, even after every conceivable nervous connection had been severed. The possibility that it was the hydrochloric acid of the chyme, absorbed into the blood stream through the intestinal walls, that produced this effect was eliminated by experiment; injecting dilute hydrochloric acid into the blood produced no appropriate effect. When, however, they scraped mucosa from the duodenal wall of one animal, ground it up with sand and dilute hydrochloric acid in a mortar, neutralized and filtered it, and tested the result, they found that they had obtained a substance that produced the observed results. To quote Bayliss, "This extract was injected into a vein [of another experimental animal], and we were naturally delighted to find that a copious flow of pancreatic juice was the result."

In the 40 years since secretin was discovered, a great amount of information has been gained about the existence and functions of a rather large number of other hormones. Various glandular structures within the body had been known to be in some way essential for life, although they had no known part in any recognized physiological system. Certain of these were now discovered to be endocrine glands. Other organs, such as the pancreas, already known to perform essential roles in body processes, were found also to produce important hormones. There still remain a number of glandular tissues of uncertain function; investigation of these and the search for additional hormones that may be produced by better known glands is still in progress. In spite of all that has been learned, we are still very far from a complete understanding of hormones and their functioning.

The deciphering of the body's endocrine control is beset with special difficulties. For one thing, the amount of hormone secreted by a gland (although sufficient to produce the normal stimulation or inhibition of bodily function) is very small, and it is difficult to obtain a sufficient quantity for study. Moreover, many of the endocrine glands are located deep within other vital tissues and are difficult to reach surgically without producing death in the experimental animal. Much of our present information has had to be obtained by removing some gland, suspected of producing a hormone, from an experimental animal and then comparing the functioning of this animal with one that remains intact. If the animal that has had a gland removed shows specific symptoms and if these symptoms can be alleviated by feeding or injecting the experimental animal with extracts taken from the same glands of other individuals, the existence of an endocrine function is indicated. The next step is to obtain a sufficient quantity of the secretion and to isolate the essential substance. If possible, this substance is purified, and its chemical composition and structure are determined. In the case of adrenalin (epinephrin), thyroxin, testosterone, and other important hormones, such knowledge is now sufficient to permit synthetic manufacture. These and other hormones that as yet must be obtained from the glands of fish or sheep or other animals are already an important part of the "medicines" available to the modern physician.

Another difficulty in precisely determining the role of any given hormone is that the endocrine glands appear to be particularly susceptible to the influence of other hormones. Removal or disease of one endocrine gland may markedly affect the functioning of another that has no obvious connection with it. Investigation of the pituitary gland, for example, is complicated by the fact that not only is it situated in one of the most inaccessible regions in the whole body (within the skull and beneath the

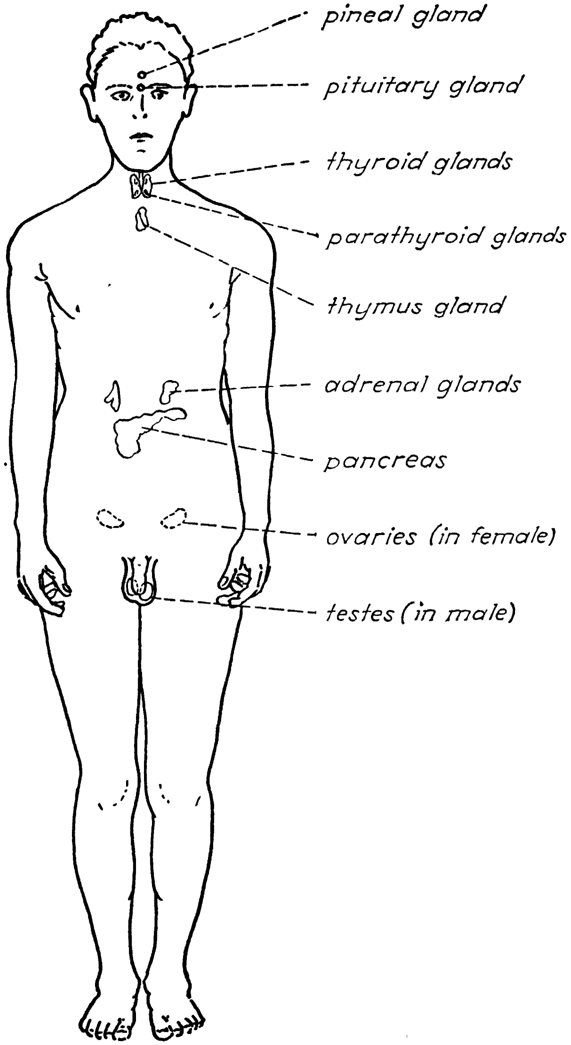
pineal gland
pituitary gland
thyroid glands
parathyroid glands
thymus gland
adrenal glands
pancreas
ovaries (in female)
testes (in male)

FIG. 51. *The location of the principal endocrine glands.* (*Redrawn from Atlas of Human Anatomy, Williams, Frohse, Brodel, and Schlossberg, Barnes & Noble, Inc.*)

brain stem) but it produces several hormones that, in large part, regulate the output and functional rhythms of several endocrine glands that are located in totally different regions of the body. Again, not all types of endocrine control are in continuous operation. Some are particularly active in early life, others show a rhythm associated with sexual changes, and still others are largely quiescent except when stimulated by way of the autonomic nervous system.

In the account that follows, some of the more important endocrine glands and the hormones that they produce are listed and briefly discussed.

The ***pituitary body*** is a small mass of tissue, about the size of a pea, that lies in a bony pocket in the floor of the skull. Morphologically, it consists of three lobes that are closely fused but different in structure—the posterior lobe being derived from an outgrowth of the floor of the diencephalon, the intermediate and anterior lobes from a pouch from the roof of the mouth of the developing embryo. The anterior lobe produces two groups of hormones, one influencing growth, the other regulating metabolic processes; the intermediate lobe produces two hormones, the functions of which are not well known in man; and the posterior lobe produces two very active hormones, *pitressin* and *pitocin.* The more important or better known of the pituitary hormones are the following:

1. *The somatotropic or growth hormone of the anterior lobe* stimulates body growth. A deficiency of this hormone in childhood results in the development of a dwarf. (If such individuals are recognized and receive injections of anterior lobe extracts early enough, normal growth may be produced or approximated.) Such dwarfs are normal mentally, become sexually mature, and have a well-proportioned body form, very different from the cretin dwarfs that result from lack of thyroid secretion. Overactive production of the somatotropic hormone in childhood results in *gigantism;* but when it does not occur until after adult stature has been reached, it results in the disproportionate development of the jaws, arms, and legs and so produces the condition known as *acromegaly.*

2. *The thyrotropic hormone of the anterior lobe* stimulates the thyroid gland and causes it to produce thyroxin. Apparently it is essential for thyroid functioning, even though the thyroid itself is normal.

3. *The adrenotropic hormone of the anterior lobe* has much the same relationship to the functioning of the adrenal cortex as the thyrotropic hormone has to the thyroid.

4. *The gonadotropic hormones of the anterior lobe* govern or influence the development of sexual maturity. In their absence, sexual maturity does not occur, and the removal of the anterior lobe of the pituitary produces an effect much like castration. These gonadotropic hormones also stimulate the production of the sex hormones in the sexually mature animal, and the fact that the sex hormones can later inhibit the production of gonadotropic hormone accounts for much of what is known of sexual periodicity and sexual rhythms.

5. *The diabetogenic hormone of the anterior lobe* aids in regulating the use of carbohydrates and fats in the body and appears to have an action that is more or less the opposite of that of the insulin, produced in the pancreas.

6. *Pitressin,* formed in the posterior lobe, acts on smooth muscles of the gut, causing them to contract; stimulates the secretion of gastric juice; acts powerfully on the kidneys; and is important in regulating the water content of the body.

7. *Pitocin,* also formed in the posterior lobe, throws the muscular wall of the uterus into strong contractions and appears to have important functions in regulating the

functioning of the uterus at childbirth. As far as known, it has no function in the male.

The ***thyroid gland*** is situated in the neck and consists of two lobes, one on either side of the trachea, connected by a thin band of thyroid tissue ventral to the trachea. Its secretion, which is well known chemically, is called *thyroxin* and is characterized by iodine content. If the thyroid glands are removed from tadpoles, they never change into frogs, if, on the other hand, very young tadpoles are given an excess of thyroxin, they metamorphose much earlier than normally, producing fully formed, minute frogs. In young human individuals, a marked thyroid deficiency results in the development of feeble-minded dwarfs called *cretins*, who frequently fail to become sexually mature. In the adult, a deficiency in thyroid gland secretion results in a lowering of the rate of basal metabolism and produces sluggish physical and mental functioning; an oversupply of secretion, on the other hand, results in loss of weight, a too great nervous activity, and other symptoms of an excessive rate of catabolism.

The ***parathyroid glands*** comprise four small bodies, two on each side, attached to or imbedded in the thyroid. Functionally they appear to be entirely independent of the thyroid and secrete a hormone, *parathromone*, which is concerned with the regulation of calcium metabolism in the body. Their removal quickly results in death. An excess of parathromone causes calcium to be removed from the bones and added to the blood and may result in the formation of calcium deposits in the kidneys, ureters, or other tissues.

The ***adrenal*** or ***suprarenal glands*** partially cap the upper end of the kidneys. Each adrenal body consists of two distinct regions, an outer cortex and an inner medulla. Each region produces a distinct hormone Although the *cortin* produced by the cortex is clearly necessary for life, its exact functions are not certainly known. It appears to be concerned in regulating the very precise balance between the various inorganic salts in the blood and body fluids and may possibly be concerned in carbohydrate metabolism

In contrast to the still uncertain function or functions of cortin, the hormone *adrenalin*, or, as it is sometimes called, *epinephrin*, produced by the medulla, is well known. To quote Amberson and Smith,[1]

"When we inject an extract of the adrenal medulla into the arm of a human being, its effects are felt almost immediately. The skin and face become pale, the heart beats more strongly but slowly, and blood pressure rises, sometimes doubling itself in a few seconds. The subject experiences a feeling of anxiety or apprehension sometimes accompanied by marked muscular tremors, an empty feeling in the pit of the stomach, and shortness of breath. All activity ceases in the stomach and intestines.

"These more obvious effects of adrenalin result chiefly from its actions upon smooth muscle. The effect of the hormone upon the stomach and intestine . . . is to inhibit their action, a change of which we become vaguely aware in consciousness. The slowing of the heart and shortness of breath are the result of carotid sinus reflexes inaugurated by the high blood pressure. If the cardiac nerves are cut in the experimental animal the effect of adrenalin injections is to speed the heart as well as to strengthen its beat, by direct chemical action. When the nerves are intact, a reflex inhibition overcomes the direct chemical effect, in the interest of preventing too high a blood pressure rise.

"Adrenalin [also] causes a transformation of muscle and liver glycogen into glucose which appears in the blood stream. The hormone is a very efficient agent for increasing the level of the blood sugar in time of crisis. It also shortens the coagulation time of the blood."

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[1] Amberson, W. R., and D. C. Smith, *Outline of Physiology*, F. S. Crofts & Co., New York, 1939

Here is a description of a body all ready to fight or to run, and the function of adrenalin is to prepare the body to meet an emergency. Transportation by the blood system is speeded up, and the blood is shunted to the skeletal muscles; the fuel for muscle use is increased, and a more abundant supply of oxyen is provided for the rapid utilization of this fuel in voluntary-muscle energy. The body is thus prepared for a maximum physical effort, and even the clotting time of the blood is shortened, in case of injury. The discharge of adrenalin into the blood is set off by emotions of fear or anger that produce impulses over the autonomic nerves going to the adrenal glands.

The pancreas. A part of the pancreas functions as a ductless gland (the remainder producing digestive enzymes as already described). The hormone produced, *insulin*, is essential for the conversion of the monosaccharides of the blood into glycogen. In the absence of insulin, the monosaccharides are excreted in the urine, and the muscles are deprived of their source of energy.

The ***pineal body,*** often classified among the endocrine glands, is a median projection of the posterior part of the roof of the diencephalon. Its secretion, which is produced before puberty, possibly inhibits premature sexual maturity.

The ***thymus gland*** is situated in the thoracic cavity above the heart. Although it may be one of the endocrines, its function is not definitely known. It contains glandular tissue until puberty, at which time the gland cells disappear. Failure of this gland to function is associated with precocious sexual maturity.

The gonads. The soma cells of the testes and ovaries produce hormones that are involved in the regulation of various sexual phenomena and body characters These will be discussed under the topic of reproduction.

CHAPTER IX

The Reproductive System

SINCE Part I of this book deals with the problems presented by organisms in their rôle as individual entities, we might logically postpone consideration of the reproductive system until, in Part II, we take up the problems of reproduction and inheritance. On the other hand, the reproductive system is intimately related to the other physiological systems of the body and profoundly affects the development, structure, and functioning of the individual. Our study of the individual organism as exemplified by man would be seriously deficient without some consideration of the influence exerted upon the individual by the reproductive organs. Later, in Chaps. XVII and XVIII, we shall again take up the reproductive mechanism, not from the standpoint of the individual of which it is a part but in relation to the production of new individuals and the maintenance of the race.

The Reproductive System of the Male. The male gametes, known as *spermatozoa*, are developed in the convoluted *seminiferous tubules* that make up the bulk of the *testis* (plural *testes*). In mammals, including man, the paired testes are suspended below the pubic region in a loose pouch, the *scrotum*, into which they descend from the abdominal cavity in late embryonic life.[1]

Certain cells of the seminiferous tubules, like the follicle cells of the ovary, nourish the germ cells while the latter are undergoing the changes that transform them into mature spermatozoa. The seminiferous tubules communicate by short ducts with a coiled tube, the *epididymis*, which lies in the scrotum alongside of the testis and, perhaps with the aid of the seminal vesicles, acts as a storehouse for the spermatozoa until they are ejected. From each epididymus a duct, the *vas deferens*, passes from the scrotum up into the abdomen, over the symphysis pubis or junction of the pubic bones, and around to the lower rear side of the bladder.

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[1] Mammalian spermatozoa are injured by the high temperatures prevailing in the abdominal cavity, and when descent of the testis fails to occur (as sometimes happens), spermatozoa are not formed.

Here it is joined by the duct of an elongated saclike *seminal vesicle*, the principal function of which is to contribute a part of the fluid that, with the spermatozoa, makes up the *semen*. Beyond this point, the vasa deferentia are called the *ejaculatory ducts;* they open a short distance beyond the neck of the bladder into the common channel for urine and semen, the *urethra*. The *prostate gland* surrounds the ejaculatory ducts and the base of the urethra and opens into the latter, as do the ducts of the small *Cowper's glands*. The functions of the prostate gland and Cowper's glands are not entirely understood, though they probably contribute fluid to the semen; they are not, however, essential for reproduction.

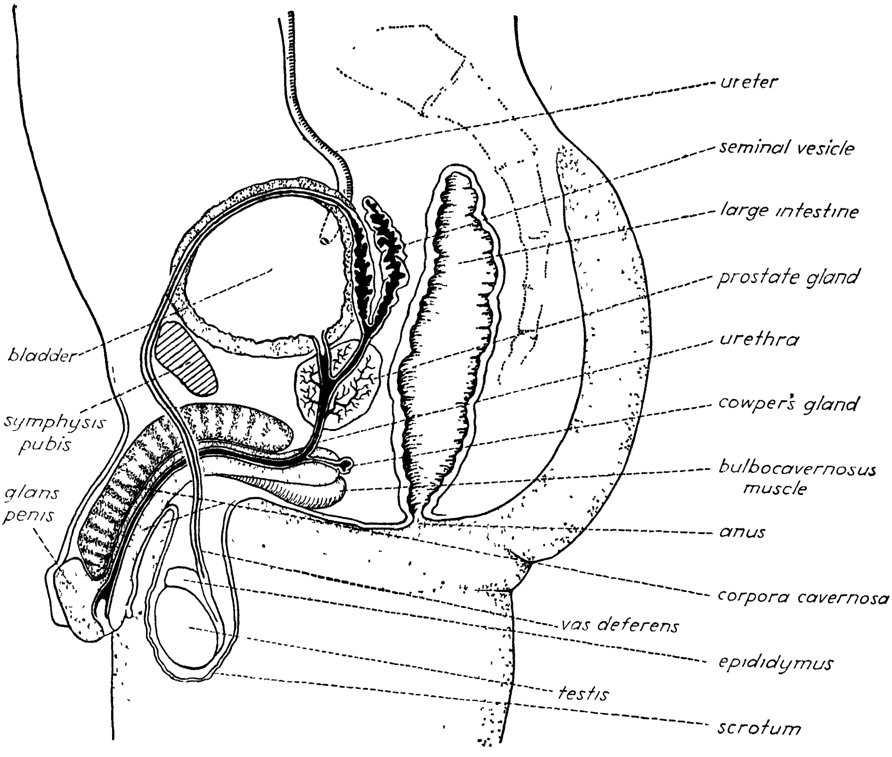
ureter
seminal vesicle
large intestine
prostate gland
urethra
cowper's gland
bulbocavernosus muscle
anus
corpora cavernosa
vas deferens
epididymus
testis
scrotum
bladder
symphysis pubis
glans penis

FIG. 52. *Diagram showing the structure of the male reproductive system.* (*Redrawn from Parshley, The Science of Human Reproduction, W. W. Norton & Company, Inc.*)

The distal portion of the urethra traverses the erectile copulatory organ, the *penis*. This organ is composed chiefly of three *corpora cavernosa*, two dorsal and one ventral, the latter enclosing the urethra and expanding at its distal end into the glans penis. The two dorsal corpora cavernosa diverge within the body and are attached to the pubic bones. The corpora cavernosa contain large blood spaces; under the influence of sexual excitement, the arteries carrying blood to the organ are dilated and the veins are constricted at its base, causing the spaces to fill with blood under pressure and the penis to become erect. Ejection of the semen is brought about chiefly by rhythmic contractions of the vasa deferentia and the bulbocavernosus muscle; the latter encloses the intrapelvic basal portion of the ventral corpus cavernosum.

The Reproductive System of the Female. The paired *ovaries* are the parts of the female reproductive system in which the germ cells are housed and in which the mature germ cells, or *eggs*, are produced. The ovaries are small, ovoid or almond-shaped bodies situated low in the abdomen and suspended in position by ligaments attached to the side walls of the pelvis and to the uterus. Like the uterus and the other abdominal organs, the ovary projects into the abdominal cavity and is covered by the peritoneum, which envelops the organ, and by its folds forms the supporting ligaments.

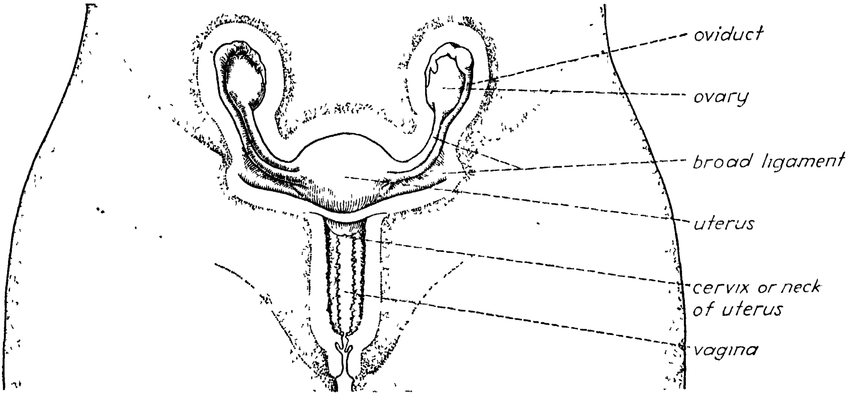

FIG. 53. *Diagrammatic anterior view of the female reproductive system.* (*Redrawn from Parshley, The Science of Human Reproduction, W. W. Norton & Company, Inc.*)

Within the ovary, the developing germ cells are surrounded by special soma or body cells that nourish them while they grow and mature. These accessory cells form a spherical structure imbedded in the ovary, known as an *ovarian follicle.* As the follicle enlarges, a split develops along one side between its inner and outer cell layers, and the space thus formed gradually fills with lymph and increases in size. When the egg is finally mature and ready to leave the ovary, it lies, surrounded by a layer of follicle cells, floating in the cavity of the much enlarged follicle. The latter has in the meanwhile pushed out to the surface of the ovary, just beneath the peritoneum that lines the peritoneal (or coelomic) cavity. The ovary has no duct for the discharge of eggs. Instead, the eggs are freed by a peculiar process called *ovulation,* which consists in rupture of the wall of the follicle and the overlying peritoneum and discharge of the follicular fluid and the egg into the peritoneal cavity.

Actually the egg does not ordinarily escape into this cavity but is discharged into or is at once picked up by the open end of the oviduct. The *oviducts* are a pair of tubes extending from the upper portion of the uterus to the vicinity of the two ovaries. There they end in enlarged, funnellike, fringed openings that communicate directly with the peritoneal cavity. The open ends of the oviducts contain smooth muscle, have some freedom of movement, and can be applied to the surfaces of the ovaries. It is probable that shortly before ovulation occurs, they cup themselves over the surface of the ovary in the region of the follicle. Even if the egg is not discharged directly into the oviduct, the currents caused by beating cilia within the funnel tend to carry it in. Rare accidents are known, however, in which eggs have escaped into the peritoneal cavity and there been fertilized; or in which the egg from one ovary has traveled to the oviduct of the opposite side, when one ovary and the opposite oviduct had previously been removed by surgery. Once in the oviduct, the egg is carried to the uterus by peristaltic waves of contraction[1] and by the beating of the cilia that line the walls of the tube.

If copulation has occurred, sperm normally meet and fertilize the egg while it is still in the oviduct. In this event, early embryonic development takes place during the several days required for passage through the oviduct to the uterus. If the egg is not fertilized, it is absorbed in the oviduct or uterus, probably through the agency of white corpuscles that pass through the walls of these organs and ingest foreign particles. In this event, there follow the phenomena of menstruation.

The ruptured follicle from which the egg has escaped soon fills with a mass of yellowish cells and becomes a gland of internal secretion called the *corpus luteum.* If fertilization does not occur, the corpus luteum persists for about 10 days and then dwindles away; but if fertilization does occur and the developing ovum becomes implanted in the uterine wall, the corpus luteum continues to grow until it reaches a diameter of about 3/4 inch by the middle of pregnancy. The corpus luteum is indispensable for successful gestation and plays an important role in the regulation of the female reproductive cycle.

The *uterus* is the organ in which embryonic development takes place. It is an unpaired, median structure with very thick muscular walls and a central cavity. The two oviducts open into its inner end, and at the outer end a narrow passage extending through the neck of the uterus communicates with the *vagina*. The walls of the uterus are lined with a vascular and glandular epithelium to which the embryo becomes attached. During pregnancy, the uterus becomes enormously enlarged, projecting far up into the abdomen. Birth of the child is accomplished by rhythmic contractions of the smooth muscles of the uterine walls, aided by the voluntary abdominal muscles. The neck of the uterus and the vagina are very distensible, and their openings are eventually stretched sufficiently to permit the passage of the child. The vagina communicates with the exterior through the urinogenital sinus, bounded by the *labia* and containing the *clitoris*, a small sensory organ homologous with the penis of the male.

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[1] *Peristalsis* is the progression of bands of constriction along a tubular organ, pushing the contents in one direction. The intestinal movements furnish a good example.

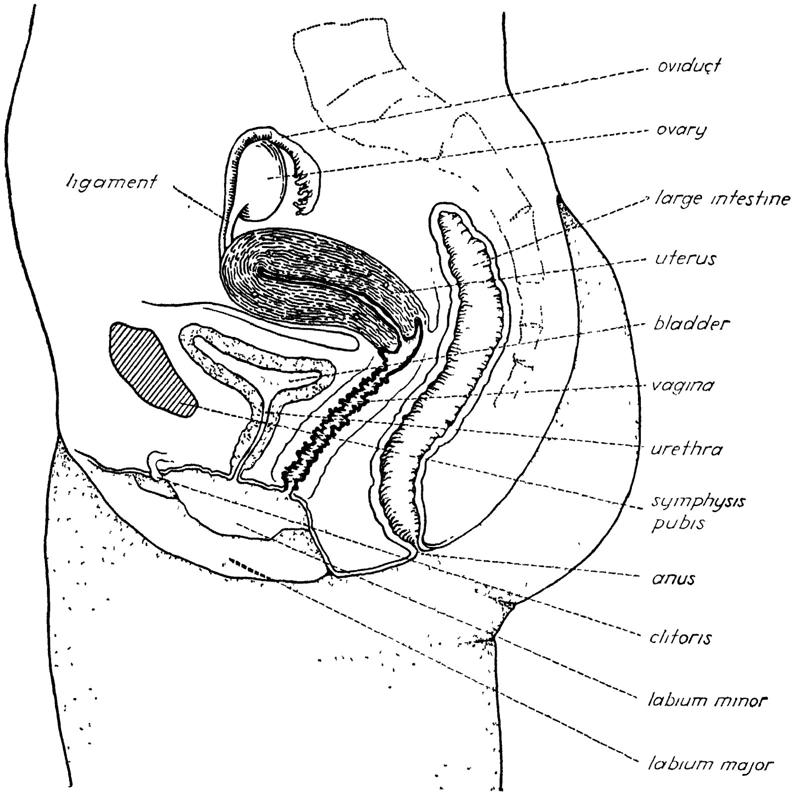

FIG. 54. *Diagrammatic lateral view of the female reproductive system.* (*Redrawn from Parshley, The Science of Human Reproduction, W. W. Norton & Company, Inc*)

Sex Hormones. We have seen something of the nature of the endocrine glands and the coordinating role played by the hormones that they produce. The testes and ovaries (*gonads*) also produce hormones, in addition to their function of nurturing the germ cells. In general, these hormones affect the development of the male and female secondary sex characters, including the differences in growth of hair, in depth of voice, and in sex instincts. They also help regulate the sex cycles, such as ovulation, menstruation, etc. The principal sex hormones and their roles are discussed below.

The Male Sex Hormone: Testosterone. The interstitial cells of the testes act as a gland of internal secretion and produce at least one male sex hormone—testosterone. This hormone has been chemically isolated and is now manufactured synthetically.

The role of testosterone can be demonstrated by noting the effects of castration (which deprives the body of the hormone) and by operations to produce sterility of such a sort that the germ cells are caused to degenerate while the remaining tissues of the testes are left intact. Certain of its effects may also be determined by injecting the hormone into normal animals (thus increasing the body amount). Injections of the hormone do not increase the rate of production of spermatozoa; in fact, they may indirectly cut it down. None of the effects of castration appear in animals in which a sterilizing operation has left the hormone-secreting tissues of the testes intact.

Secondary male sex characters are associated with testosterone. The changes in growth and distribution of body hair and in voice and stature at puberty fail to occur if the testes are removed. Castration produces somewhat large and fatter animals. In castrated adults, the seminal vesicles, prostate gland, and seminal ducts become functionless and undergo atrophy. Sexual behavior diminishes, indicating that, although much of the sexual behavior of the human male is dependent on purely psychological elements, it is undoubtedly affected by testosterone. There exist many erroneous notions about the roles of the male sex hormone and the gonads. The supposed regenerating and invigorating effects often attributed to "gland grafting"—increase in life span, and restoration of potency—may be cited as examples.

The activity of the testis, both with respect to testosterone production and to the formation of spermatozoa, is in turn under the remote control of the pituitary gland through the agency of a gonadotropic hormone. Removal of the pituitary produces effects like those of castration.

In review, the functions of the testes may be said to be:

1. Nurturing of spermatozoa (nonendocrine).
2. Production of testosterone (endocrine), which
    a. Causes (but is not always necessary for the maintenance of) male secondary sex characters.
    b. Stimulates the development and functioning of accessory sex organs (prostate gland, etc.).
    c. Contributes to sexual desire and behavior.

Female Sex Hormones and Reproductive Cycles. The ovaries produce at least two sex hormones, *theelin* and *progestin*. These hormones, with others produced elsewhere, play an important part in the reproductive cycles of the female and in the production of secondary sex characters and sexual behavior.

In the sexually mature females of all mammals, there are rhythms or cycles in the reproductive activities. Chief among these are the *oestrus* (Greek, *oistros*, "frenzy, desire") period, which occurs about the time the ripe ovum leaves the ovary, and the *menstrual* (Latin, menstruus, "monthly") period, which occurs after failure of the liberated egg to become fertilized and implanted. We have seen something of these periodicities in the discussion of the female sex organs. They may be tabulated as shown.

The complicated physiological machinery regulating the changes outlined in the following chart involves chiefly the *gonadotropic* hormones from the anterior lobe of the pituitary and the hormones formed in the ovary. Other hormones, however, also play a part in connection with secondary phases of the female reproductive mechanism, such as lactation (milk production in the breasts). It is clear, through animal experimentation, that the ovaries are a primary source of the chemical control of the various cycles.

The Ovarian Control. During the first week following menstruation, the ovum and the follicle in which it lies develop and ripen. The follicle becomes larger, and its central cavity fills with a fluid—the *follicular fluid.* This fluid contains the hormone *theelin* (or *estrone*), which enters the blood during this period in ever-increasing quantity. On approximately the eighth day, the ripe ovum is liberated into the oviducts. The follicle from which the ovum was liberated undergoes a remarkable change. As we have already seen, some of its cells enlarge and become filled with a yellowish pigment to form a body known as the *corpus luteum* (Latin, "yellow body"). If fertilization occurs, the corpus luteum lasts throughout the first 7 months of pregnancy and produces the second female sex hormone, *progestin.* If fertilization and implantation of the ovum in the uterus do not occur, the follicle with its yellow body begins to break down and is completely absorbed in about 2 weeks.

The hormone theelin is the female counterpart of the male hormone testosterone but has many more duties. It is the cause of the changes in the uterine wall following menstruation. These changes are seen in the thickening of the tissue lining the uterus, with an increasing vascular and glandular development. Thus theelin, during the first week following menstruation, conditions the uterus for the reception of the ovum. It aids in the normal development of the uterus before adolescence and maintains the uterus and accessory reproductive structures in normal condition in the adult. It supports the development of the mammary glands and maintains them in the normal adult state. It is responsible for the female secondary sex characters and contributes to the sex urge and sexual behavior.

Progestin is the hormone of pregnancy. It has no effect upon the reproductive organs until they have been influenced by theelin but thereupon completes the uterine changes started by that hormone. The membranous lining of the uterus, which was thickened by theelin, is softened and moistened through stimulation of its glands by progestin. A favorable environment for the spermatozoa and the development of the ovum is thus produced. Without the uterine changes produced by progestin, pregnancy is impossible. After the fertilized egg has been implanted and pregnancy begins, progestin aids in the establishment of the physiological readjustments that the body must make for child bearing. For example, it stimulates mammary-gland enlargement and lactation late in pregnancy.

Gonadotropic Hormones. In discussing the secretions of the anterior lobe of the pituitary, we listed, among others, the gonadotropic—or gonad-stimulating—hormones. The periodic changes in the uterus may be explained by the ebb and flow of ovarian hormones. In their turn, the ovaries are regulated from the anterior pituitary. At least two gonadotropic hormones have been demonstrated for the female. The first of these, the *follicle-stimulating hormone,* causes the growth of the ovarian follicle and the production of theelin; the second, the *luteinizing hormone,* causes the formation of the corpus luteum and the production of progestin. It is the reciprocal relations between these gonadotropic hormones and the two sex hormones that are responsible for the cyclic phenomena of the menstrual cycle. As the concentration of theelin in the blood increases to a maximum at the time of ovulation, the follicle-stimulating hormone is correspondingly repressed; then, with the occurrence of menstruation, theelin production falls off abruptly, releasing the anterior pituitary from inhibition and thus causing a rise in the output of the gonadotropic

THE REPRODUCTIVE CYCLE IN THE HUMAN FEMALE[1]

Days after menstruation stops	*Ovaries*		*Lining of uterus*
	Follicle and ovum	*Corpus luteum*	
1st to 7th	Gradual ripening of ovum and increase in quantity of follicular fluid	Absent	Resting condition, then increasing thickness of lining with increased vascularity and gland formation
About 8th. . .	Ovulation and passage of ovum into oviduct (where fertilization may occur. Sperm entering oviduct 2 to 3 days before ovulation *may* remain and fertilize the egg)	Forms from the cells of the ruptured follicle	Uterine glands begin to secrete a viscid fluid
9th to 14th	Arrival of ovum in uterus	Grows	Ready for reception of fertilized ovum
Alternatives: (*a*) If fertilization has not occurred			
14th to 24th	Ovum can probably no longer be fertilized and disintegrates	Gradually disappears	Secretion subsides
24th to 28th	New follicle begins to develop in ovary	Absent	Menstruation—uterine lining sloughs off, with moderate bleeding
(*b*) If fertilization has occurred			
14th to 280th. . .	No follicle formation or ovulation during pregnancy	Remains during first 7 months of pregnancy	Fertilized ovum imbeds itself in uterine wall and grows

[1] Modified from *The Machinery of the Body*, by A. J. Carlson and Victor Johnson, courtesy of the University of Chicago Press. All figures are approximate and vary from individual to individual.

hormone. This stimulates the progress of follicle development and starts the next cycle. A similar reciprocal relation evidently exists between progestin and the luteinizing hormone.[1]

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[1] In the male, the stimulating effect of the gonadotropic hormone on the production of spermatozoa by the testes is less apparent, except in those mammals in which there is a marked seasonal periodicity.

The activity of the breasts is also under hormonal control. One of the effects of theelin and progestin is the enlargement of the breasts and increase in their glandular tissue that occurs during pregnancy. The actual inception of lactation, however, is caused by another hormone produced in the anterior lobe of the pituitary, *prolactin*. So long as either theelin or progestin are present in large amount the production of prolactin is inhibited. After the birth of the child, however, prolactin is produced, and milk secretion begins in about three days. Continued secretion of this hormone is necessary for continued lactation; this is apparently brought about by nervous impulses arising from sensory stimulation of the nipples in nursing.

CHAPTER X

The Organization of the Individual Plant

In our study of the problems presented by the individual organism, we have thus far been concerned with the animal type of organization, as exemplified by man. We have looked at the structure and functioning of the human body in some detail, seeking to learn what its problems of maintenance are and how they are met. Animals are only one of the two great divisions of life, however; it is now time for us to examine the very different scheme of individual organization that has been developed among plants.

All the higher forms of life, including those organisms most familiar to us, are either animals or plants, and this fundamental dichotomy among living things extends far down the scale of organization. Not until we reach certain of the lowly unicellular forms of life does the distinction between plant and animal become obscure—and this in spite of the tremendous diversity in size, form, and mode of life exhibited by the members of the two groups. In what, then, does the difference consist? What fundamental characteristic makes one organism an animal, another a plant? In final analysis, if we ignore for the moment all superficial differences and all exceptional cases, it comes down to this—that animals *capture* their food ready made, whereas plants *manufacture* their food from simple chemical substances. The most important structural and functional differences between plants and animals are attributable to the unlike requirements of their methods of nutrition.

We shall best be able to comprehend the way in which the individual plant is built and functions by analyzing some representative plant type in detail, just as we did in the case of the human body. For this purpose, we shall choose not some single species of plant but a group of the flowering plants called the *dicotyledons.* In the case of the human body, we are interested in all its details per se, because they are a part of ourselves; but we are not so vitally concerned with the minor features of individual plant species, and by treating the group as a whole, we can select the best examples or generalize for the entire group and thus obtain a more comprehensive picture of the structure and functioning of the average flowering plant.

The dicotyledons are those flowering plants that have two cotyledons (seed leaves) in the seed, net-veined leaves, and flower parts usually in fours or fives. This group includes a great many familiar plants. As examples, we may cite such trees as oak, pecan, sweet gum, apple, and orange; such shrubs as oleander, wax myrtle, blackberry, blueberry, and gallberry; such vines as woodbine, grape, and poison ivy; and such herbs as tomato, tobacco, carrot, bean, cabbage, clover, poppy, dog fennel, dandelion, thistle, and goldenrod.[1] Even this small number of examples is sufficient to show how great a range in size, form, and growth habit exists among the dicotyledons; yet in spite of their superficial diversity, the members of this group all share a basic structural and functional pattern that we shall soon proceed to examine.

COMPARISON OF PLANT AND ANIMAL ORGANIZATION

Before entering our detailed study of the individual plant, it will be well for us to look more closely at the principal similarities and differences between animals and plants and thus clarify our conception of the plant type of organization and some of its basic requirements, limitations, and peculiar features. It has already been pointed out that the most essential difference lies in the method of nutrition, plants making their food and animals obtaining it directly or indirectly from plants. We shall see how the requirements of food manufacture account for all the most important features of plant structure except those relating to reproduction.

Features Common to Plants and Animals. Like animals, plants are made up of cells and cell products. The protoplasm of plant cells resembles that of animal cells in appearance and properties and in nearly all plants is similarly differentiated into nucleus (or nuclear material) and cytoplasm. Each cell of the plant, like that of the animal, is

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[1] The flowering plants, or *angiosperms*, have two great subdivisions—the *dicotyledons*, mentioned above, and the *monocotyledons*, the members of which have only one seed leaf, parallel leaf veins, and flower parts usually in threes or multiples of three. The grasses, palms, lilies, orchids, and many other familiar plants are monocotyledons. The angiosperms are placed with the *gymnosperms* (pines, cycads, etc.) to form the phylum Spermatophyta, or seed plants—the highest of the four plant phyla. None of the remaining types of plant produces seeds; they form the three lower plant phyla (Pteridophyta, or ferns and fern allies; Bryophyta, or liverworts and mosses; and Thallophyta, or algae, fungi, lichens, bacteria, etc.). The members of these three lower phyla are simpler in structure than the seed plants and differ more or less markedly from the structural and functional pattern here described. Their features of organization are briefly discussed in a following section, and a more detailed treatment of plant classification will be found in the Appendix.

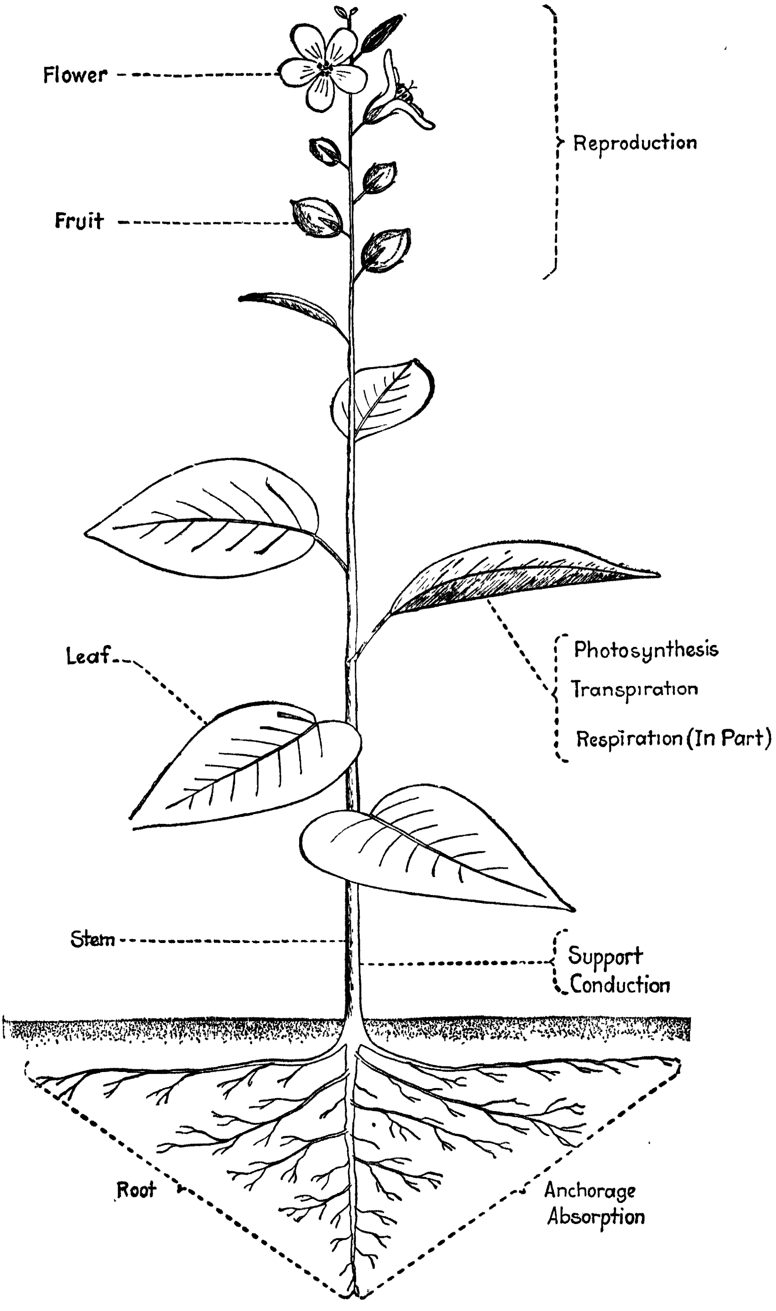
Flower
Fruit
Reproduction
Leaf
Photosynthesis
Transpiration
Respiration (In Part)
Stem
Support
Conduction
Root
Anchorage
Absorption

FIG. 55. *Diagram to show the important structures and functions of a seed plant. Contrast with those of the human body, as shown in Fig. 8. (From Sinnott, Botany: Principles and Problems.)*

bounded externally by a living cell membrane. Unlike most animal cells, the cells of plants are also usually enclosed in a more or less rigid, nonliving cell wall secreted by the cell; but this is not an essential difference, since some plant cells are naked, whereas some animal cells, such as those of bone and cartilage, are similarly enclosed by a nonliving cell product. The cell wall of most plant cells is composed of *cellulose*, a substance chemically related to starch. The cell membrane is normally held in close contact with the inner surface of the cell wall by osmotic pressure within the cell, but the cell can be made to shrink away from the cell wall by immersion in a concentrated salt or sugar solution. Many animal cells contain liquid-filled vacuoles; in plant cells, the vacuoles are often so large as to occupy most of the space within the cell, the living protoplasm lining the cell walls or sometimes extending through the vacuoles as protoplasmic strands. Plant cells divide by mitosis just as animal cells do, except that in most plant cells, there are no centrosomes, and the division of the cytoplasm in the telophase is usually accompanied by the formation of a cell-wall plate between the daughter cells.

Cell differentiation and division of labor are as marked among plants as among animals. The cells of the higher plants are of many types, each specialized for the performance of a particular function. As in animals, similar cells are grouped into tissues, and the tissues are, in turn, built into organs and systems of organs adapted for carrying out major functions. The organization of the plant body is less complex than that of the higher animals, in conformity with the greater simplicity of its tasks, but it rests upon the same basis—the orderly cooperation of a multitude of living units, the cells, each of which has some small part to play that is related to the functioning of the whole organism.

The plant is confronted by the same fundamental problems as the animal. These are (1) the *maintenance of the individual*, in the first place, by the capture, transformation, storage and utilization of energy and materials; in the second place, through devices for protection against unfavorable factors in the environment, both physical and biotic; and (2) the *maintenance of the race*, through reproduction. The second of these problems constitutes the theme of a later part of the book; here it suffices to call attention to the fact that the ends to be attained are the same for both animals and plants, no matter how different the means by which they are accomplished.

Some Important Differences between Plants and Animals. The most obvious and characteristic features of the higher plants, including the division of the plant body into root, stem, and leaf, its relative immobility and rigidity, and the prevailingly green color of the foliage, are all directly related to the method of food getting. All green plants[1] owe their color to the presence in their cells of the complex substance called *chlorophyll*, which functions as a catalyst.[2] In the presence of chlorophyll, the energy of sunlight causes carbon dioxide and water to combine into the simple sugar, *glucose*, which is the basic plant food (not the carbon dioxide, water, and minerals taken in by the plant, as is sometimes stated). The process of glucose manufacture is called *photosynthesis* (Greek, *phos*, *photo*, "light" and *synthesis*, "putting together"). Organisms may be divided into two great groups according to whether they do or do not possess chlorophyll and in consequence can or cannot manufacture their food. Only the green plants belong to the first group, having chlorophyll; practically all other organisms, including the multicellular animals, the Protozoa, and certain plants that have lost the ability to produce chlorophyll, must obtain their food directly or indirectly from green plants.

A typical animal, in order to obtain food, must be able to move about, to recognize and secure the food, and to rework it into a form suitable for its own use. Furthermore, the existence of other food-seeking organisms necessitates some means of offsetting or escaping from their attentions. Related to these needs is the general development among animals of locomotor and sensory devices, complex coordinative mechanisms, and digestive apparatus, all of which are largely without counterparts among plants.

The requirements of the green plant are fundamentally different. Typically, it must have an extensive absorptive (root) surface for taking in water and dissolved inorganic substances. It must also have a large chlorophyll-bearing (leaf) surface exposed to light for the capture of energy for photosynthesis, and to air (or water), for obtaining the necessary carbon dioxide. The relatively great expanse of surface that these requirements necessitate simplifies the problem of respiration and eliminates need for an elaborate breathing mechanism, but introduces other problems in the use and control of evaporation of water. Since the light, water, carbon dioxide, and minerals that the plant requires are almost everywhere available, locomotion is inessential and is largely precluded by the necessity for a root system. Rigidity and strength are called for in order to support the necessary leaf spread. A digestive system is unnecessary, since the food is manufactured within the cells and is either used at once or stored in simple and easily altered forms; but a transporting system is necessary to carry inorganic substances, food, water, and the products of metabolism to different parts of the plant. The by-products of photosynthesis (oxygen) and of food oxidation for release of energy (carbon dioxide) are themselves substances necessary for plant metabolism and are more or less completely re-utilized. Since the residues of these processes are gaseous and are able to transfuse through the leaf surfaces and since few liquid or solid wastes are produced, no specialized excretory mechanism is required. Coordination of the

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[1] Some "green" plants appear to be of other colors than green, because of the presence of masking pigments in addition to chlorophyll. The true antithesis of the "green" plants is found in certain plants that lack chlorophyll.

[2] A *catalyst* is a substance in the presence of which a specific chemical reaction takes place that would otherwise occur slowly or not at all. The catalytic agent takes part in the reaction but does not itself enter into permanent combination with the reacting substances. An enzyme is a catalyst produced as a result of cellular activity but independent of the presence of living cells in its operation. According to this definition, chlorophyll is not an enzyme, since photosynthesis is not produced by chlorophyll extracts nor by isolated chloroplasts but occurs only in intact cells.

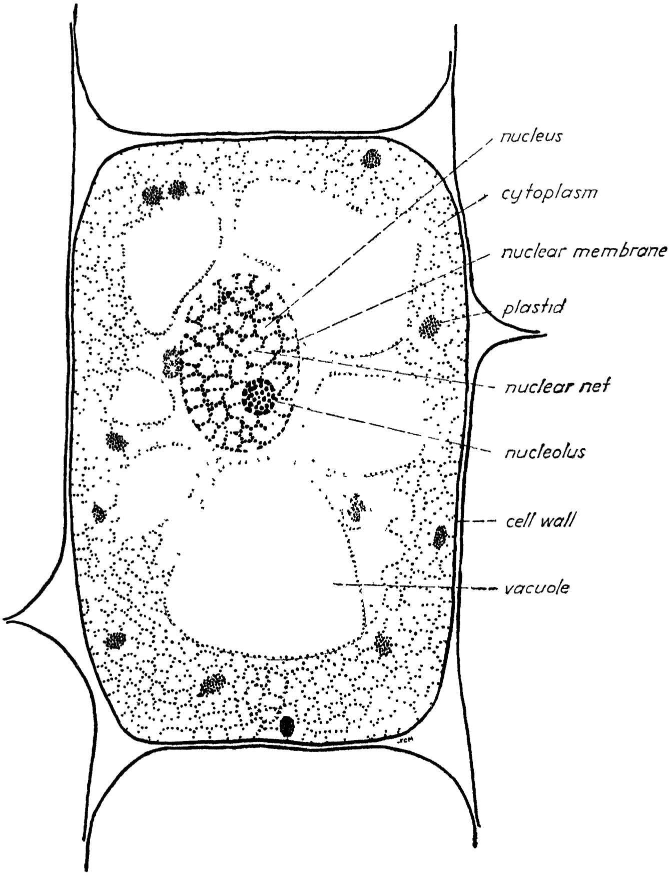

FIG. 56. *A typical plant cell (from the waterweed Elodea). (Redrawn from Sinnott, Botany: Principles and Problems.)*

activities of the various parts of the plant is simple and largely under direct chemico-physical control; hence the plant has developed no complex nervous system or highly specialized sense organs.

The Indeterminate Scheme of Plant Growth. A second major difference between the higher plants and the metazoan animals is the method of growth characteristic of the former. In the higher plants, zones of active growth lie everywhere beneath the surface—at the ends of the branches, at the root tips, and forming a sheath, the *cambium*, around the branches, stem, and roots. The cells of these zones remain always young, unspecialized, and similar in characteristics and potentialities to those of the embryonic plant. Together these growth zones constitute the *meristem*. Throughout the active life of the plant, the cells of the meristem continue to reproduce, giving rise to new tissues and causing the plant to increase in size. The cell layers thus produced are added to those previously present, and the individual cells cut off from the meristem become specialized for particular functions according to their location in the plant. Many tropical plants grow throughout the year; in these, the meristem is active until the death of the plant. More often, especially in temperate regions, growth takes place chiefly during the spring and summer; the meristem actively produces new tissues at this time but goes into a resting condition during the remainder of the year.

As a result of the indeterminate scheme of growth of the plant, the structure of the growing tip of a branch or root is not the same as that of an older part of the same branch or root. The growing point is actually in an embryonic state, and the degree of maturity of structure increases proportionately with the distance from that point. This situation makes it advisable to treat the development, structure, and functioning of the plant together.

GENERAL ORGANIZATION OF THE PLANT

The Seed and the Embryo. All the highest plants produce special reproductive bodies called *seeds*, and the group derives its scientific name from this characteristic—Spermatophyta (Greek, *sperma*, "seed" and *phyton*, "plant"). Seeds are not eggs; they are embryonic plants enclosed in tough *seed coats*. By the time the seed is ripe, the embryo has developed far enough so that the principal parts of the body of the plant can be distinguished. In the dicotyledons, of which the bean may be taken as an example, the greater part of the seed generally is made up of two greatly swollen leaves (*cotyledons*), filled with a store of starchy food that carries the developing plant through the period of germination and establishment. The cotyledons enclose and partly conceal the rudiments of the rest of the plant; these rudiments are the *radicle* or embryonic root, the *hypocotyl* or embryonic stem, and the *plumule* or embryonic leaf shoot. The entire embryo is in a resting state, with all metabolic activities reduced to a very low point.

Germination. Under proper conditions of moisture and temperature, the embryonic plant becomes active and begins to grow. The seed coat splits, and the radicle and plumule emerge. The elongating radicle is *positively geotropic* and *negatively phototropic*—*i.e.*, it turns toward the center of the earth under the influence of gravity and away from light. Thus, regardless of the position in which the seed may happen to lie, the developing root will always tend to penetrate the soil instead of growing upward or sideways. As the radicle pushes downward, the elongating hypocotyl, bearing the cotyledons and plumule, grows upward,[1] its reactions being just opposite to those of the radicle. Upon emerging into the light, the cotyledons, together with the rest of the free parts of the plant, become green. This enables them to assist the plumule and stem in manufacturing food, besides yielding the store that they already possess. As the developing leaves take over food manufacture, the cotyledons waste away and are ultimately shed.

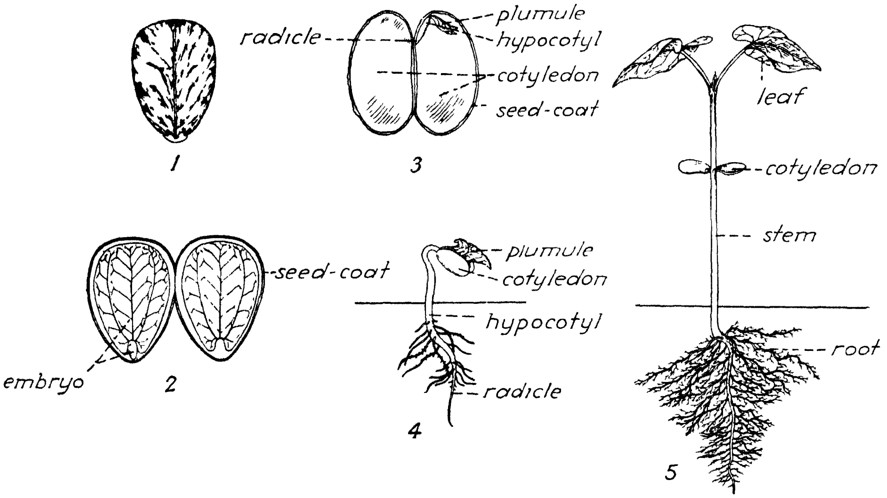

FIG. 57. *Germination of the bean.* (*1*) *Castor bean;* (*2*) *castor bean split open;* (*3*) *common bean split open;* (*4*) *young bean seedling;* (*5*) *older bean seedling.* (*Courtesy of the General Biological Supply Company.*)

The ***principal parts of the plant body*** are already differentiated in the seed—*root* and *stem* (which together form the *axis*) and *leaves.* These parts are analogous to the organs of a higher animal, since each consists of many types of specialized cells grouped into tissues and since the arrangement of the tissues is such as to fit the entire structure for the performance of specific tasks. The roots anchor the plant, take in soil water and its dissolved substances, and store manufactured food. The stem supports the leaf spread and transports water and other raw materials to, and manufactured food away from, the leaves; it is often also a storage place for food. The leaves capture the energy of sunlight and use it to manufacture food, act as the chief organs of respiration, and largely control the evaporation of water. The *flower* and the *fruit* are organs adapted to the purposes of reproduction. *Buds* are embryonic leaf and flower shoots in a state of arrested development, awaiting the advent of favorable conditions; in this respect, they resemble the resting embryo in the seed. Like the seed, they are enclosed in a resistant coat, in this instance composed of overlapping scales.

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[1] In many plants, however, only the plumule emerges from the ground, the hypocotyl and cotyledons remaining buried.

CHAPTER XI

Roots and Their Functions

In popular usage, the term *root* is applied to any part of a plant that is normally below the surface of the ground. Strictly speaking, however, not all subterranean plant structures are roots, and not all roots are subterranean. A true root may be recognized by a number of characteristics: it does not possess nodes bearing leaves or leaf buds; its tip is covered by a special structure, the root cap; the internal arrangement of its tissues differs from that of a stem; and it generally possesses root hairs in a zone just back of its tip. The branches of roots do not develop from buds, as do those of stems, but originate from a definite zone within the root and have to push their way out through the overlying tissues to reach the surface.

A typical root is almost cylindrical, tapering gently from the base to the free end. The root cap at its tip protects the delicate tissues of the growing point from abrasion as the root pushes through the soil. The zone of root hairs a short distance behind the root tip is the region where absorption of soil solutions occurs. Back of this zone, the root does not increase in length but only in thickness; the primary functions of this older part of the root are the conduction of absorbed materials, anchorage of the plant, and the production of branch roots.

The radicle of the seed develops into the primary root, which tends to grow straight downward. In many plants, this primary root gives rise to the entire root system, by sending off secondary lateral roots. These develop in regular succession from above downward; since they originate in a definite position within the primary root (generally opposite the xylem masses, described below), they tend to be arranged in longitudinal rows. True forking of roots is unknown in the higher plants, though subsequent enlargement of some of the branch roots may simulate forking. In plants where the primary root continues to elongate, producing lateral branch roots in regular succession (an inverted counterpart of the conical trunk-and-branch pattern often seen in the aerial parts of plants), the arrangement is called a *tap-root system*, exemplified in pine, dandelion, clover, and carrot. When the primary root soon ceases to grow and the major part of the root system is formed from many thin, nearly equal branch roots developed from its short axis, we have what is known as a *fibrous root system,* as in many grasses. Other types of root

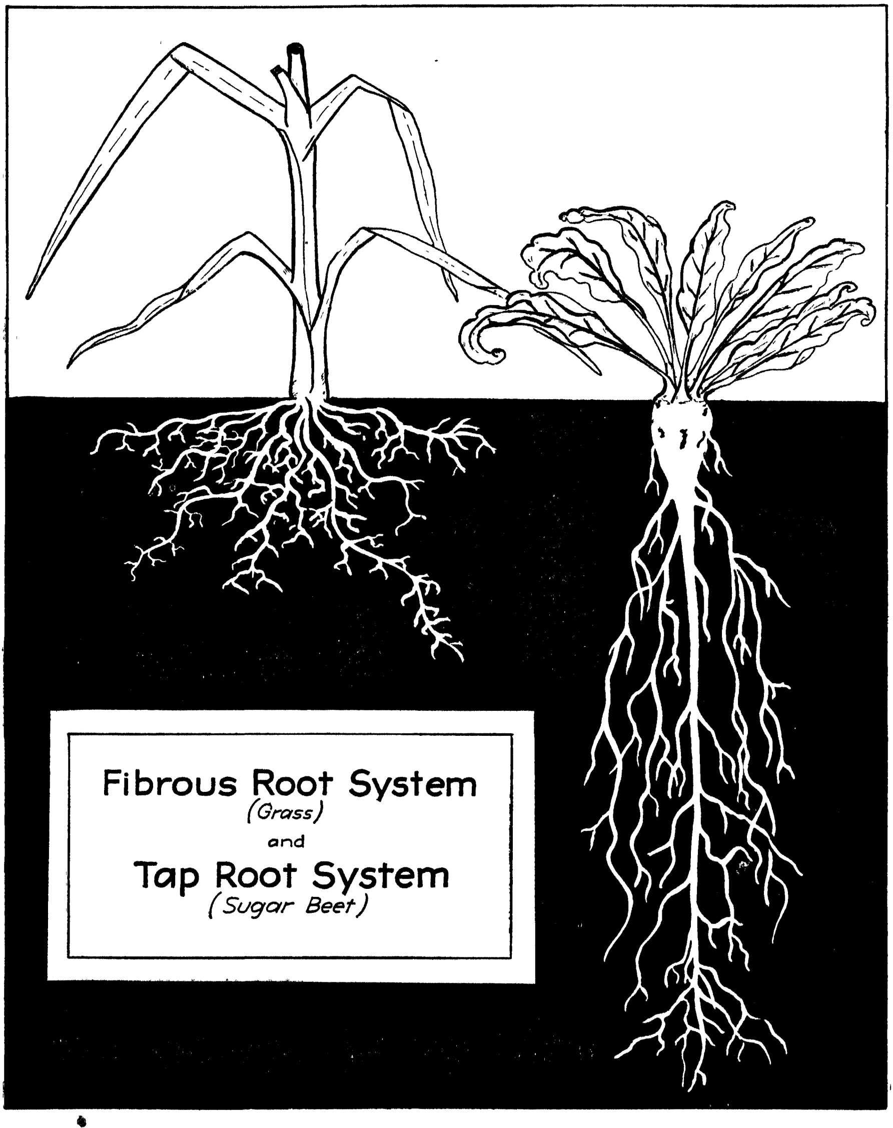

FIG. 58. *Fibrous and tap-root systems of plants. In the fibrous root system of the grass (left) the roots are all rather slender, much branched, and shallow. In the tap-root system of the sugar beet (right) there is a single large, deep root from which lateral roots arise.*

systems also exist. In many plants, the primary root system is supplemented or superseded by the development of numerous *adventitious* or accessory roots, which may develop from any part of a plant. They are especially numerous on underground stems but may also arise from the leaf nodes of aerial stems or even from leaves themselves.

The Root Tip. The apical portion of the root as far back as the base of the zone of root hairs (generally 1½ to 2 inches in length) constitutes the root tip. This is the part of the root that grows in length, produces new tissues, and carries on absorption of soil moisture and dissolved substances. Beginning at the apex, four regions may be recognized in the root tip: the *root cap*, the *growing point*, the *region of elongation*, and the *region of maturation or zone of root hairs.*

The *growing point* is a part of the meristem. It is composed of embryonic tissue—undifferentiated cells that grow and divide very rapidly. The divisions occur mostly at right angles to the axis of the root, so that cells are cut off from the meristematic zone on the side toward the tip of the root and also on the side toward the base. Those produced on the side toward the tip are added to the root cap and make good the constant loss of its outer layers caused by abrasion. Those cut off on the side toward the base of the root are destined to form the various tissues of the mature root. Between these two regions of differentiating daughter cells, the parent meristematic zone remains as the persistent growing point, continuously shifted forward by its own active cell division.

As the growing point advances away from the cells cut off behind it, those cells first elongate and later begin to broaden out and to differentiate into the various sorts of tissue cells characteristic of the fully formed root. This sequence of changes is responsible for the zonal arrangement of the cells of the root tip. The surface layer of cells forms the *epidermis*, one cell in thickness. These cells are roughly cuboidal in shape and are thin-walled. By the time the zone of elongation has progressed beyond any given group of epidermal cells, they have produced delicate tubular outgrowths, the *root hairs*, from a fraction of a millimeter to a centimeter in length, closed at the free ends. Thus the surface of the zone of differentiation that follows the region of elongation becomes clothed with a dense growth of root hairs, which penetrate the soil crevices and absorb water and dissolved substances through their thin walls. The region from the root cap to the beginning of the root-hair zone is also absorptive, but its surface is so small, compared to that of the mass of root hairs, that the latter are many hundredfold as effective. As the root grows forward, new root hairs are continually produced at the *distal*[1] border of the root-hair zone, and those at the *proximal*[1] border die. Behind the region of root hairs, the surface of the root becomes nonabsorptive because of the deposition in the walls of the epidermal cells of a corky substance called *suberin* (from *Quercus suber*, the "cork oak")—the same material that makes cork so impenetrable to water.

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[1] These terms are useful in describing position and direction in relation to pro-

The Structure of a Young Root. The arrangement of tissues in the root is best seen in a cross section through the region of root hairs, where the cells produced by the growing point have become differentiated into

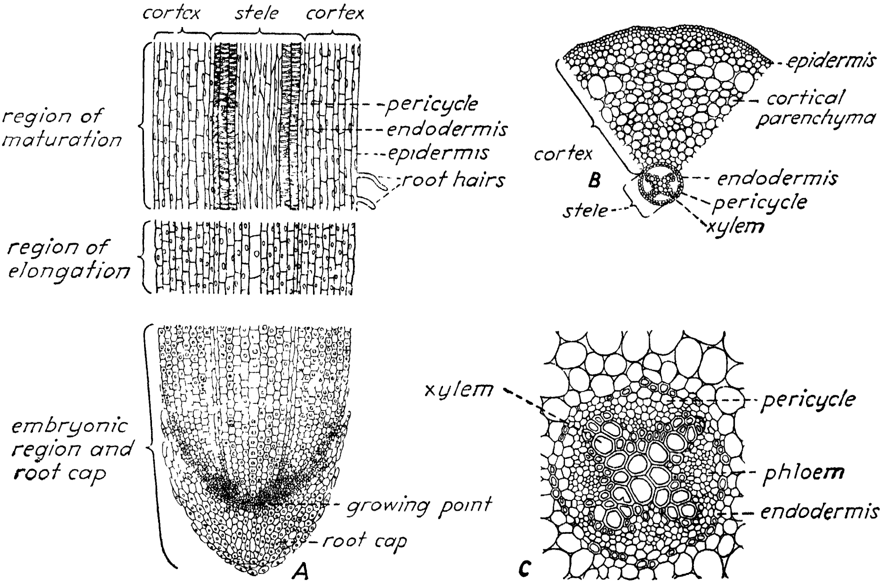
cortex
stele
cortex
region of maturation
pericycle
endodermis
epidermis
root hairs
region of elongation
embryonic region and root cap
growing point
root cap
A
epidermis
cortical parenchyma
cortex
B
endodermis
pericycle
stele
xylem
xylem
pericycle
phloem
endodermis
C

FIG. 59. *Structure of a dicotyledonous root.* (*A*) *Longitudinal section of root tip;* (*B*) *portion of a cross section of the root in the region of maturation;* (*C*) *cross section of the stele and surrounding structures, more highly magnified.* (*Courtesy of the General Biological Supply Company.*)

tissue cells but where complications due to secondary thickening have not yet entered. At the surface is the *epidermis*, with its root hairs. Beneath the epidermis is a zone called the *cortex*. Most of the cortex is composed of a spongy tissue called *parenchyma*, made up of rounded cells with thin walls and large vacuoles; but the cells of the innermost layer of cortex have thickened walls, and this layer, which surrounds the stele, is called the *endodermis*.

The inner core of the root, including everything inside the cortex, comprises the *stele*. Its outermost layer is a cylinder of parenchyma cells

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jecting structures, such as an arm or a plant root. The tip is the *distal end*, the attached base the *proximal end;* but with reference to any point along the structure, *distal* means the direction away from the base; *proximal*, the direction away from the free end.

called the *pericycle,* which gives rise to branch roots and which in perennial plants plays a part in the radial growth of the root. Beneath the pericycle, the stele contains the vascular system, the cambium layer, when one is present, and sometimes a central pith and groups of fibers that add to the strength of the root.

The *vascular system* consists of two specialized types of tissue which together form the transporting or conductive system of the plant. One of these, the *xylem,* is essentially a structure of thick-walled dead cells, so arranged and connected as to function as water conduits. The other tissue, the *phloem,* is composed of living cells connected through openings in the cell walls. In the phloem, substances in solution pass through the protoplasm from cell to cell. The structure and functions of these vascular tissues are more fully treated in dealing with the stem. In a cross section of a young dicotyledonous root, the xylem forms a star-shaped figure with three, four, or five rays; it generally extends to the center of the root. The strands of phloem lie between the rays of the xylem star, separated from the xylem by parenchyma; in cross section, they appear as small, isolated cell groups.

The Structure of Older Roots. In many plants, including most annuals, the roots do not increase in thickness. In such plants, the structure of the older parts of the root does not differ in any essential respect from that just described, and such roots lack a cambium layer. In perennial plants, on the other hand, the year-by-year growth of the whole plant makes necessary additional support by the roots and an increase in the capacity of the vascular system. The roots of such plants grow in diameter with age.

This is made possible by the presence of the meristematic layer called the *cambium.* The cells that lie between the arms of the xylem star and the phloem strands (and which become parenchyma in the roots of annual plants), in perennials retain their meristematic properties and constitute a *cambium layer.* The cambium forms a fluted cylinder (a wavy circle in cross section), extending out around the ends of the xylem star and separating the xylem from the phloem strands, so that the xylem is inside the cambium and the phloem is outside. Like the cells of the growing point, those of the cambium layer are undifferentiated and are capable of rapid growth and division. In the region between the xylem arms and the phloem, the cells cut off on the side toward the xylem become xylem; those cut off on the side toward the phloem become phloem. Where the cambium layer bends around the arms of the xylem star, it produces neither xylem nor phloem but only parenchyma cells.

As this growth process goes on, the cambium ring (or cylinder) smooths out. Between the arms of the original xylem star there grow out masses of *secondary xylem,* separated by rays of parenchyma opposite the arms of the star. The original phloem is pushed out toward the periphery of the growing root and may be crumpled up and destroyed by the pressure of the developing secondary phloem and xylem. The *secondary phloem* lies just outside the masses of secondary xylem, separated from them by the cambium ring.

While this thickening has been going on, the pericycle (also composed of parenchyma) has again taken on the functions of meristem and has formed a second cambium layer (the *cork cambium*) outside the first. This cambium produces a layer of cork cells, the walls of which are impervious to water because they contain suberin. The cork layer cuts off the cortex from access to food and water, causing it to die and disappear. Thus the older parts of the root come to consist solely of the greatly modified stele, with a covering of corky bark instead of the original epidermis.

THE FUNCTIONING OF THE ROOT

The Soil as the Environment of Roots. The soil consists of a porous mass of large and small mineral grains, together with a variable proportion of organic material derived from the decay of plant and animal bodies and animal excreta. Its deeper parts are more or less saturated with water, but in the upper layers, the spaces between the grains are filled with air. In the minute passages and cavities of this aerated zone live innumerable bacteria and simple plants, engaged in decomposing the organic debris. Here also live minute animals of extraordinary diversity, so numerous that their excrement and their dead bodies form important constituents of the soil materials. In this zone, each mineral grain is coated with a colloidal film of organic or inorganic material and enclosed in a thin layer of water that contains from 0.1 to 1.0 per cent of various dissolved substances, including those essential to plants.

Substances Taken in by the Roots. Aside from carbon dioxide and oxygen, which are discussed later, the various inorganic substances upon which plant metabolism is dependent are obtained from the soil. Water enters largely into the composition of all protoplasm and cell products. It is one of the two substances from which the basic plant food glucose is manufactured. It carries in solution the other materials used by plants. Lastly, it maintains the internal pressure (*turgor*) within the cells of the plant, which is responsible for much of the stiffness and strength of the plant body and furnishes a mechanism for the movement of various parts of the plant. The very large amounts of water used by plants are almost wholly obtained from the soil, with some minor exceptions (aquatic plants, epiphytes, parasites, and plants living in other unusual situations).

Besides carbon dioxide and water, plants need *nitrogen, phosphorus, sulphur, potassium,* and *sodium* for the synthesis of fats and proteins from glucose and its derivatives, and for the building of protoplasm. These elements are absorbed from the soil in the form of dissolved salts—*nitrates, phosphates, sulphates,* and *salts of ammonia.* Besides these, minute amounts of a number of other substances are normally found in plant tissues. They were long thought to be only accidentally present or, in any event, to be of negligible importance. On the contrary, some of them, at least, are now known to be essential to the health or even to the life of the plant. If the elements *magnesium, calcium, iron, manganese, boron, zinc, copper* (and perhaps others) are not available to the plant in minimal quantities (the required amounts varying for different plants), the plant will sicken and may die.

Many formerly obscure plant diseases have recently been traced to deficiency of one or more of these "trace" elements in certain soils, and the ailments so caused have come to be known as *mineral-deficiency diseases.* They are much more prevalent in certain regions than in others on account of differences in the mineral content of the soils. In the Atlantic coastal plain, the soils have been largely derived from materials carried to the sea by ancient streams. The sorting of these sediments by rivers and waves and the leaching to which the derived soils have been subjected have left many soils in this area deficient in certain elements—particularly manganese, zinc, and copper. The deficiencies are especially marked in Florida, which lies farthest from the sources of these materials in the Piedmont and Appalachian districts and which has unusually heavy rainfall to cause leaching. The part played by the "trace" elements in the physiology of the plant is only partly understood, though the problem is being actively studied.

Intake and Transportation by Roots. The root hairs penetrate into the crevices of the soil, pressing close against the surfaces of the soil particles. These are wet with soil moisture—a dilute solution of inorganic salts. Water and some of the solutes pass through the permeable walls and the semipermeable cytoplasmic cell membranes into the root hairs of the epidermal cells. Just what causes this to occur is still something of a mystery, though in part the factors responsible are well known. In considering the familiar phenomenon of absorption by roots, it is once more borne in upon us how close at hand the frontiers of science lie and how much remains to be learned of even the commonest processes of life.

The epidermal cells with their root hairs may be thought of as immersed in the dilute soil solution and separated from it by the living cytoplasmic membrane that bounds the cell. (The cell wall may be ignored in this connection, since it is freely permeable.) The cell membrane, being semipermeable, permits water to pass readily in either direction but offers resistance to the passage of solutes. In spite of the latter effect, the dissolved substances do enter the cell, but they are found within it in widely different concentrations than in the soil solution. Some substances continue to enter the cell until the concentration may reach 25 or even 40 times that in the solution outside the cell, whereas others show a lower concentration within the cell than without. Simple diffusion will obviously not account for such selective absorption, and it is no explanation to say that the cell actively takes in certain substances and tends to exclude others. Though it appears to do just this, there must be some physical mechanism involved, and we do not understand how it is accomplished. As one author puts it, "The living plasma membrane . . . must be of a very peculiar nature."

When we have passed over this difficulty, the remaining steps of the absorptive process are somewhat better understood, though they still present a sufficiency of unsolved problems. The concentration of solutes within the plant cell causes water to pass by osmosis from the dilute soil solution into the cell, thus creating *osmotic pressure* within the cell. The cell expands and presses against the cell wall. When the restraining pressure exerted by the cell wall becomes great enough to equal the osmotic pressure, the cell cannot expand further and cannot take in more water. The force with which water tends to be drawn into (or, strictly speaking, to enter) the cell may be termed the *suction pressure.* Obviously the suction pressure is not simply the osmotic pressure; it is measured by the osmotic pressure less the restraining pressure exerted by the cell wall, and tends to diminish to zero as the cell becomes engorged with water to the limit permitted by the cell wall. In the instance of the root hairs and delicate epidermal cells, absorption of water would soon reduce the suction pressure to nothing, even if the osmotic pressure did not rupture their thin walls, if water were not at the same time being withdrawn from them by some means.

The mechanism for such withdrawal and for producing a continuous flow across the cortex to the stele is found in the gradient of increasing osmotic pressures that exists from the epidermal tissues to those of the stele, together with the mechanical suction pressure exerted by the transpiration pull. In some plants, it has been found that the cells of the innermost layer of the cortical parenchyma have about four times the osmotic pressure of the epidermal cells. This means that each layer of cells exerts suction pressure on those toward the outside of the root, while at the same time it loses water to the next inner layer of cells. As a result of this, plus the effects of the transpiration pull, soil water continuously enters the root hairs and passes across the cortex to the vicinity of the vascular tissues in the stele. Here the water is pulled into the xylem and is carried along the roots and up the stem to the leaves. The suction pressure causing the water to enter the xylem tubes is evidently not the result of osmosis, since it has to overcome the high osmotic pressures within the cells surrounding the xylem. Instead it appears to be wholly a matter of the transpiration pull exerted by the leaves; this is discussed in the next chapter in connection with the functioning of the vascular tissues. There is evidence that most of the dissolved substances imbibed with the soil water are not carried in the xylem, but are passed along to the rest of the plant largely through the living cell chains of the phloem.

CHAPTER XII

Stems and Their Functions

STEMS vary more than roots, both in form and in details of structure. They may be thick, strong, and relatively rigid, like those of trees; delicate and succulent, like those of many herbs; long, slender, flexible, and tough, as in vines; rootlike and subterranean, as in dewberry and Solomon's-seal; or they may modified in a variety of other ways. Although they somewhat resemble roots in the arrangement of their tissues and share with them the functions of support and transportation, they show numerous striking differences from roots. They normally have no absorptive function and lack epidermal structures corresponding to the root hairs; the apical growing point is not protected by a cap of cells; their outgrowths (leaves and branches) are restricted to definite parts of the stem separated by leafless and branchless intervals, and these outgrowths develop from surface buds instead of pushing out from the pericycle. The arrangement of the vascular tissues in the stele is also somewhat different from that of roots.

Certain important characteristics of stems may be most easily comprehended by study of deciduous trees or shrubs, *i.e.*, those which shed their leaves at the end of the growing season. While the leaves are still on the tree, it may be noted that they are all attached to the short terminal portions of the branches; such leaf-bearing shoots are called *twigs*. All parts back of the twigs constitute the trunk and its branches. When the leaves are shed in the fall, a *leaf scar* marks the former position of each, and it can then easily be seen that just above each leaf scar there is a bud. The buds situated along the sides of the twig occur singly or in pairs or whorls, according to the particular habit of the tree; they are called *axillary buds*, because each arises in an *axil*, or angle between a leaf petiole and the twig (cf. Latin, *axilla*, "armpit"). At the tip of the twig is a *terminal bud*. Each bud contains a rudimentary twig, already bearing rudimentary leaves. This delicate embryonic structure is enclosed and protected by overlapping, waxy *bud scales*, which are regarded as modified leaves.

With resumption of activity by the tree in the spring, the terminal bud and one or more of the axillary buds (generally those nearest the tip) begin to swell with the rapid growth of the enclosed structures. The bud scales then open, and the young shoot pushes out. It elongates rapidly, chiefly by lengthening of the *internodes,* or intervals between the regions where leaves and axillary buds develop, which are called the *nodes.* Soon the shoot appears as a replica of last year's twig; the latter no longer bears leaves and has become a part of the branch. The bud scales at the base of the new twig drop off after a time, leaving a group of *bud-scale scars;* the space between two such groups of scars marks the amount of growth accomplished in one season, and each section of the branch between two groups of bud-scale scars was originally an embryonic shoot inside a bud.

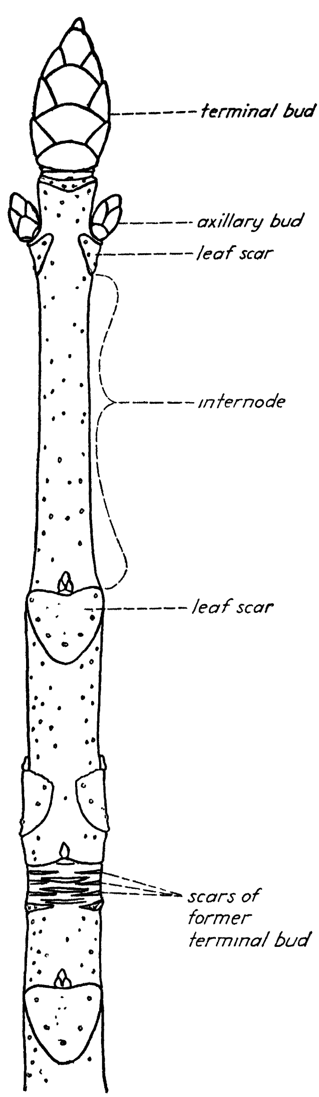

FIG. 60. *A woody twig (horse chestnut) in winter condition, to illustrate the principal external features of the stem. (Redrawn from Sinnott, Botany: Principles and Problems.)*

The Structure of a Bud. From the facts described above, it is evident that each bud contains a growing point. In fact, the bud, or stem tip, resembles the root tip in fundamental respects. Its growing point is apical, instead of being covered by a cap of cells, as in the root; but in both stem and root, the meristematic zone is followed first by a region of elongating cells and then by a region of cell differentiation in which the tissue groups are formed. On the other hand, roots possess nothing corresponding to the nodes and internodes of stems, nor does the internal structure of roots and stems correspond in all details.

The Structure of the Young Woody Stem. There are three principal types of stem structure among the spermatophytes: (1) the *woody stem of the dicotyledonous trees and shrubs* (to which the stem of pines and their relatives is essentially similar), (2) the *succulent stem* *of the herbaceous dicotyledons,* and (3) the *very differently organized stem of the monocotyledons* (the palms, grasses, lilies, etc.). The following account applies especially to the first of these, the woody dicotyledonous-gymnosperm type; the features of the other two can be mentioned only briefly.

A cross section of a one-year-old branch (stem) of such a tree as an oak shows the following arrangement of tissues. The surface is covered with a layer of *epidermis,* one cell thick. The outer surfaces of the epidermal cells are protected by a thin layer of *cutin* (a waxy substance related to suberin and, like the latter, impervious to water). Beneath the epidermis lies the *cortex,* extending inward as far as the stele. The outer layers of the cortex are usually composed of elongated cells with thickened corners, forming a type of mechanical or supporting tissue called *collenchyma.* Within this zone, the cortex is made up of parenchyma, sometimes with the innermost cell layer differentiated into an *endodermis* composed of mechanical tissue.

Inside the cortex is the central cylinder, or *stele.* The stele of the stem differs from that of the root in having a central *pith* of large or small diameter, enclosed in a cylinder of *vascular tissue,*[1] the outer surface of which is bounded by the pericycle. The inner portion of the vascular cylinder is composed of xylem; the outer part, of phloem, with a thin cambium layer between.

The Structure and Growth of Older Stems. Lengthening of the stem and its branches is entirely the result of the growth of the twigs. As soon as a twig is fully developed, it ceases to elongate and henceforth increases only in diameter. Its radial growth is accomplished primarily by the activities of the cambium lying between the xylem and phloem. The cells of the cambium layer are mostly tall and slender, and the layer itself is normally only one cell thick. Except for the occasional radial divisions that enable the cambium cylinder to enlarge with the growth of the stem, the cambium cells always divide parallel to the surface of the stem. One of the two cells produced at the division remains a part of the cambium; the other, if on the inside, becomes a xylem cell; if on the outside, a phloem cell. Usually several layers of xylem cells are produced for each layer of phloem.

Besides the ordinary tall cambium cells that produce the vertically elongated cells of the vascular tissues, the cambium contains other cells that are radially elongated. These generally occur in groups, forming vertical bands or streaks in the cambium cylinder one to several cells wide and sometimes as much as several inches high. These groups of

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[1] The vascular cylinder may be complete or may be interrupted by *pith rays* extending from the central pith to the cortex; the former condition is that here described.

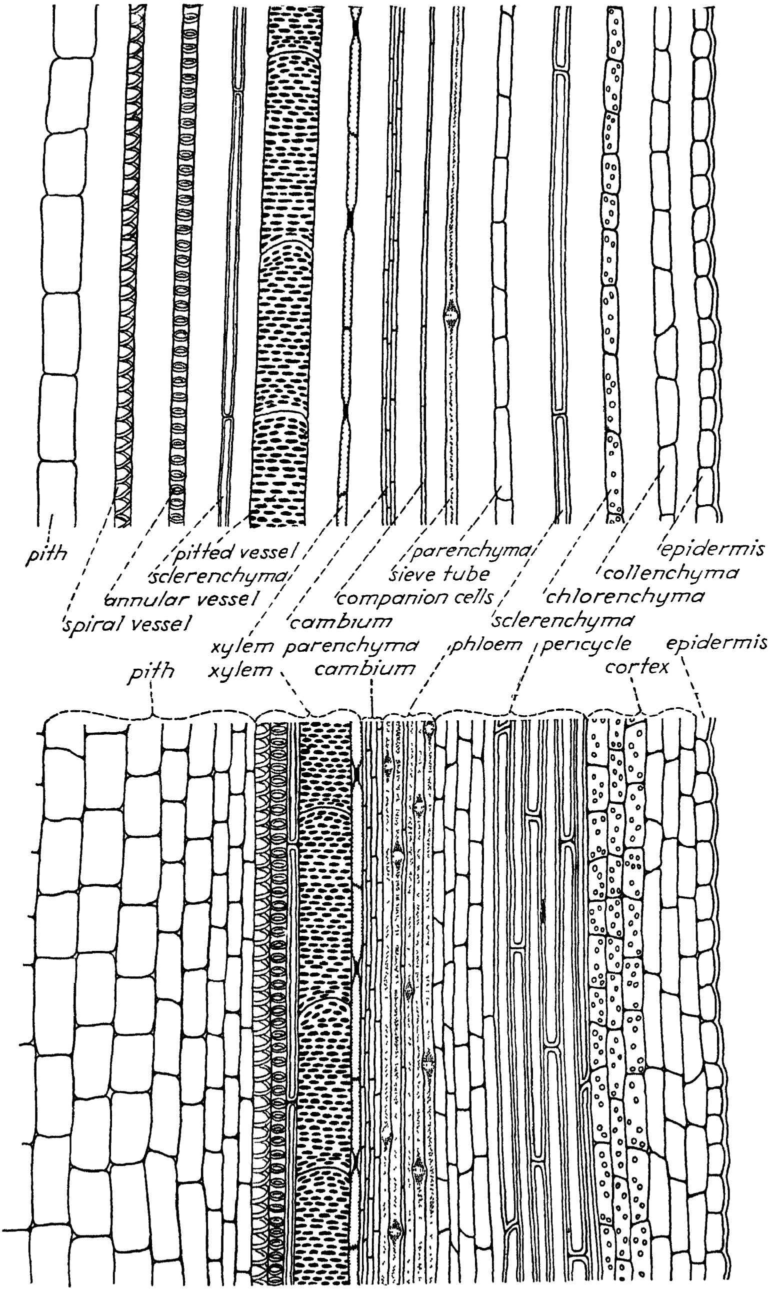
pith
pitted vessel
parenchyma
epidermis
sclerenchyma
sieve tube
collenchyma
annular vessel
companion cells
chlorenchyma
spiral vessel
cambium
sclerenchyma
xylem parenchyma
phloem
pericycle
epidermis
pith
xylem
cambium
cortex

FIG. 61. *Longitudinal section of a portion of a dicotyledonous stem. The lower drawing shows the stem as it appears with the various tissues in place. The upper figure represents the various tissues separated to illustrate the nature of the cells composing them. (From Brown, The Plant Kingdom, by the courtesy of Mrs. Mary A. Brown.)*

special cells constitute the *ray cambium* and give rise to radial rays of parenchyma cells called the *vascular rays.* Since parenchyma cells are cut off from the ray cambium alternately on the inner and outer sides, the same ray extends both into the xylem and into the phloem. The thin-walled cells of which the rays are composed permit radial transfer of water and dissolved materials between xylem and phloem. As the diameter of the stem increases, new groups of ray-cambium cells form between the original ones, so that no cells of the stele are far from one of these rays.

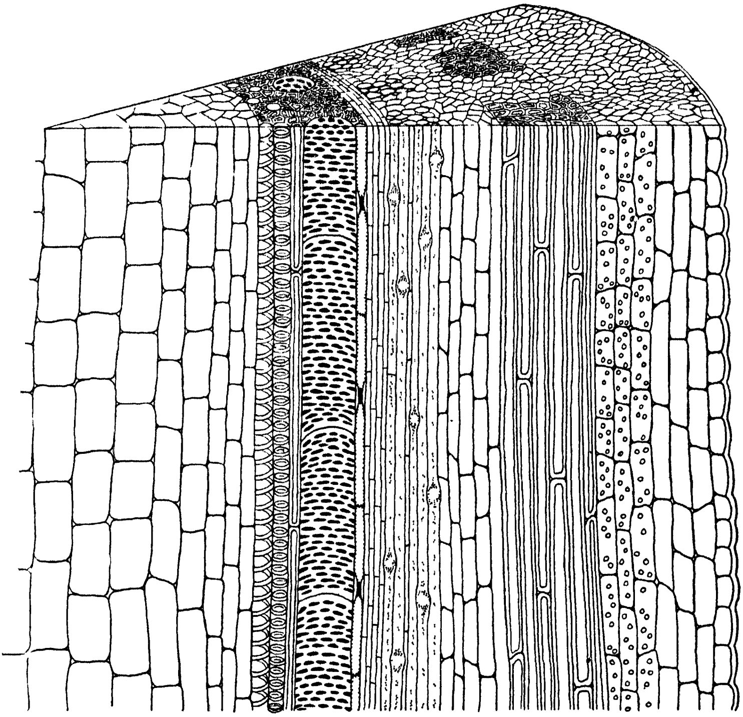

FIG. 62. *Diagrammatic longitudinal and cross sections of the dicotyledonous stem shown in Fig. 61.* (*From Brown, The Plant Kingdom, the courtesy of Mrs. Mary A. Brown.*)

The wood of the stem is the xylem. In most trees of the temperate zone, the cambium is most active in the spring and then produces numerous large xylem cells; such spring wood is porous and light and usually contains many vessels large enough to be seen with the unaided eye as minute pores on a cross section of the wood. Later in the season, the cambium becomes less active, and the summer wood then formed is made up of much smaller cells with relatively thick walls; it is denser and usually darker in color than the spring wood. Because of the regular alternation of seasons, the wood comes to be made up of concentric cylinders (rings, in cross section) of spring and summer wood. A pair of such layers constitutes an *annual ring*,[1] and the age in years of any particular part of the tree may be determined by counting them. In tropical regions with uniform temperature and rainfall throughout the year, most trees do not produce annual rings; but any regular alternation of favorable and unfavorable conditions, such as wet and dry seasons, results in their formation. Another well-known feature of the xylem is its differentiation into heartwood and sapwood in many trees. The *heartwood* is the older, central portion of the xylem. It no longer functions as part of the vascular system, for its cells have become impregnated and darkened with resins and tannin, increasing its density and strength but blocking the water channels. It is thus transformed into an exclusively mechanical tissue. The *sapwood* is the younger outer portion of the xylem; its main function is water transport.

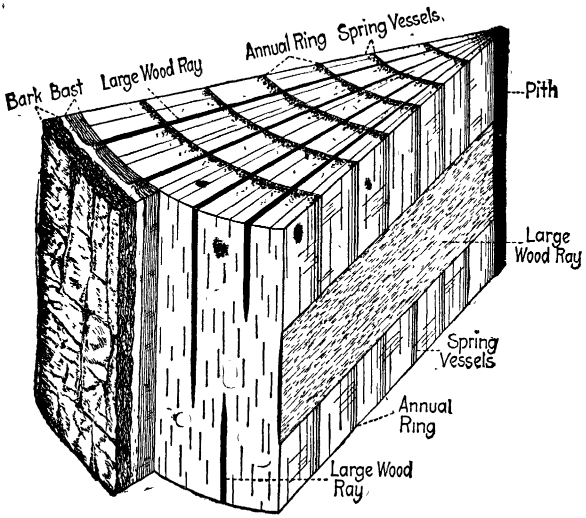

FIG. 63. *A segment of an oak log.* (*From Sinnott, Botany· Principles and Problems.*)

The "bark" of the stem is made up of all the tissues that lie outside of the xylem—the phloem, the cortex, and (in younger stems) the epidermis. It can readily be stripped from the wood, since the layer of delicate, thin-walled cambium cells is easily ruptured; "peeling" a stem destroys the cambium.

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[1] The figure or pattern seen on the cut surfaces of wood is caused by the annual rings—narrow parallel stripes if the log was sawed radially, broad bands or parabolas or ellipses if the log was cut tangentially.

The phloem is added to from the inside by the action of the cambium. As the diameter of the wood increases, the original ring of phloem becomes too small to encircle the stem, and it breaks apart. But since the cambium, by radial cell division, keeps pace with the growth of the xylem cylinder and always forms a continuous layer, the new phloem produced at any given stage of growth forms a sheath just large enough to enclose the cambium and xylem at that time. The discontinuous and crumpled remnants of the earlier phloem layers are forced outward by the increase of the xylem and phloem beneath them, and the spaces between the segments of the interrupted layer of old phloem become filled with cortical parenchyma.

Beneath the original epidermis, there develops a *cork cambium,* as in the case of the root, and the impermeable layer of cork cells produced by this cambium causes the death of the epidermis. In smooth-barked trees, the original cork cambium continues indefinitely to serve as the outer protective layer of the stem, increasing in diameter as the trunk enlarges and renewing the thin cork layer that imperceptibly crumbles off from the surface. In rough-barked trees, on the other hand, deeper layers of cork cambium form one after another beneath the first, each causing the death of all cells outside it by cutting off their supply of water and food. This process converts more and more of the original cortex into dead outer bark and results in the formation of a thick protective covering, the surface of which scales off or is fissured into ridges as the trunk increases in diameter. When the successively deeper zones of cork formation finally invade the outer and older layers of the phloem, the trunk comes to consist solely of the stele. New layers of phloem, continually formed by the cambium, replace those lost to the outer bark.

Other Types of Stem Structure. The type of stem just described is that characteristic of the woody dicotyledons, of which the hardwood trees are typical. The stem of the gymnosperms (pines and their allies) is very similar, differing chiefly in that the xylem is composed almost entirely of tracheids, without vessels but generally with resin ducts, and that the sieve tubes of the phloem are not accompanied by companion cells.

The stems of herbaceous dicotyledons, such as the bean and thistle, are similar to those of the woody dicotyledons, except that the amount of vascular tissue is relatively less and the pith and cortex relatively greater in extent, and that the vascular ring is usually broken up by pith rays into a number of separate vascular bundles arranged in a ring around the pith. Each of these vascular bundles is like a segment of the vascular ring of the typical woody dicotyledon stem, containing a cambium layer and hence being capable of growth; it is therefore called an *open bundle,* in contrast to the type of bundle found in the monocotyledons.

The type of stem developed by the monocotyledons (for example, the grasses, maize, lilies, and palms) is very different from the other two types. The meristematic zone in the growing point is almost as great in diameter as the mature stem. It gives rise to an outer epidermal layer, within which is a narrow zone that corresponds to the cortex and pericycle of the dicotyledonous stem and which is often strengthened with mechanical tissue. The rest of the interior of the stem tip is composed largely of parenchyma cells, among which are scattered strands of cambium, most numerous toward the outside. These cambium strands differentiate into phloem on the outside and xylem on the inside, as in the dicotyledonous stem, but *the whole of the cambium is thus transformed;* in the mature stem, none remains in the meristematic condition, and the completed bundles, being incapable of growth, are called *closed bundles.* The xylem and phloem produced by the original cambium strands must function throughout the life of the plant, and the total quantity of vascular tissue cannot be increased. Growth in diameter of the stem is usually slight and is caused almost entirely by increase in the breadth of the individual cells left behind by the meristem of the growing point.

THE FUNCTIONING OF THE STEM

The functions of the stem are primarily two—*support* of the leaf spread and *transportation* of materials between leaves and roots by the xylem and phloem, which together make up the vascular system. Support is afforded largely by the various mechanical tissues, aided by the turgor produced in cells by osmotic pressure. In young dicotyledonous stems, the outer cylinder of collenchyma adds stiffness to the structure, but the strength of older stems resides almost wholly in the xylem.

The Xylem, or Wood. Xylem consists almost entirely of mechanical and conductive tissues. The first of these is made up of *fibers,* which are elongated cells with very thick walls strengthened by deposits of an impermeable substance called *lignin.* The walls of these cells become so thick and impervious that the enclosed cell finally dies, and the space that it occupied is nearly obliterated. Masses of these lifeless fibers form the strongest mechanical tissue developed by the plant, called *sclerenchyma.* The sclerenchyma forms longitudinal strands in the xylem, and so does not hinder the transport of water. The conductive tissue is made up of two principal types of conducting cells. The *tracheids* are spindle-shaped, relatively short, and have their walls pitted so that water can flow from one to another; they are arranged in long strands of overlapping cells. The *vessels* (tracheal tubes) are rows of much larger cells, called *tracheae* (singular, *trachea);* these are arranged in vertical rows, and the end walls of the cells are perforated or dissolved away, so that each row of tracheae functions as a continuous tube. The protoplasm of both tracheids and tracheae dies and disintegrates after secreting the cell walls; it is only after the death of the cells that formed them that the lifeless cell walls form functional conduits for water transport.

The great volume of water needed to make good the constant loss by evaporation from the leaves is carried almost wholly by the tracheids and vessels of the xylem. This tissue forms a one-way transporting system from roots to leaves. If the phloem of a stem is cut through without injury to the xylem, the leaves do not wilt, though such girdling eventually results in the death of the plant from causes discussed below; but if the xylem is cut across with as little injury as possible to the phloem,[1] the leaves wilt very rapidly, showing that it is the xylem and not the phloem that carries the great bulk of the water that they require.

The ***upward movement of water through the xylem*** is an easily observable phenomenon, whose causes are not immediately evident. We have to seek a mechanism capable not only of holding up a column of water to great heights—as much as 300 feet in the case of the American sequoia or the Australian blue gum tree—but also of driving (or pulling) many gallons of water a day to this height. The water flows through ducts of extremely small diameter, the walls of which are wettable; *capillary attraction* could therefore account for the rise of water to a height of perhaps 30 feet, though it would not account for its continued upward flow. The *osmotic pressure* developed in roots has recently been shown to be far greater than was previously supposed, but the root pressures would have to be literally enormous and far greater than they actually are to drive water to the top of a tall tree, even aided by capillarity. Doubtless both these factors play a part in the process, although the flow of water is most rapid in the summer, not in the spring, when root pressures are highest.

The principal cause of the upward movement of water in the plant seems to be *transpiration pull*—an actual pulling force exerted from above and transmitted along the water columns—not in the way that air is "pulled" into the lungs, rushing into a region of lowered pressure, but in the way that a wire transmits a pull through its tensile strength. It has been found that a fluid such as water, if free of air bubbles and enclosed in a rigid tube to the wall of which it adheres, can transmit a very considerable tension through the cohesion of the water molecules. Confined by the walls of the vessel, the fluid is unable to change its shape and behaves in some respects like a solid; under these circumstances, a force equal to more than 200 and perhaps more than 300 times atmospheric pressure is required to rupture the water column. The water occupying the xylem channels seems to fulfil these conditions, adhering to the rigid walls of the vessels and tracheids and therefore able to transmit any pull exerted on the water threads from above. The cross walls present in the xylem channels do not interfere with the practical continuity of the water columns, being themselves saturated with water.

As explained in the next chapter, water is continually being lost by evaporation (transpiration) from the cells surrounding the air chambers in the leaf; their suction pressure consequently rises, and they take water from the adjoining cells; these, in turn, take water from the tracheids in the fine vascular bundles (veins) of the leaf. The water columns in these dead tracheids are continuous with those in the rest of the xylem of the plant, and as a result of the withdrawal of water from the leaf tracheids, these columns are placed in a state of tension that is transmitted throughout the plant and thus to the roots. The transpiration pull is there felt by the cortical cells adjoining the xylem strands, and water is drawn from them into the xylem. This, in turn, increases the suction pressure of the cortical cells and, in combination with the osmotic gradient mentioned in the discussion of the root, leads eventually to the intake of water from the soil by the root hairs.

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[1] This operation is very difficult to perform and has no practical applications.

There are certain difficulties in the way of accepting this as the whole story of water intake and transportation in the plant, but it is the most satisfactory explanation yet arrived at and accounts for most of the observed phenomena. The water columns, established by capillarity or root pressure while the plant is small, are continuously maintained and pulled upward during the growth of the plant like so many slender wires hanging suspended from the leaf surfaces. In this way, they can be lifted hundreds of feet above the ground. The reality of the transpiration pull can be demonstrated by cutting into the base of a tree, whereupon air enters the cut ends of the tubes and follows the water columns as they are drawn upward. The development of air bubbles in any great number of the xylem conduits would seriously diminish the flow of water and result in wilting and death of the plant, and how this is prevented or overcome is still an unsolved problem.

The Phloem. Unlike the xylem, the phloem is composed mainly of living cells. The principal conducting elements are the *sieve tubes*—vertical rows of large cells with perforated side and end walls through which protoplasmic strands connect one cell with the next. In many instances, the mature cells lack nuclei. Along the side of each sieve-tube cell (except in the gymnosperms), there extends a slender, delicate companion cell of uncertain function. Movement of water and dissolved substances through the sieve tubes evidently results largely from diffusion or protoplasmic transfer and hence is much slower than the flow of water in the xylem conduits.

The phloem, in contrast to the xylem, constitutes a two-way transporting system. It serves to carry inorganic raw materials from the roots to the leaves and manufactured food substances in both directions—downward from the leaves to the stem and roots for use and storage, and upward from temporary storage in the roots and stem. Although it was long believed that the combined nitrogen, potassium, and other raw materials taken in with the soil water were carried up in the xylem, recent experiments indicate that the phloem carries most of these materials and that the xylem is almost wholly restricted to the transport of water. Proteins and simpler nitrogenous compounds are abundant in the sieve tubes, and it is probable that transfer of these is one of the chief functions of the tubes. Since movement of materials in the phloem is by transfer through the protoplasm and not by a current, one substance may be moving toward the roots, simultaneously with the leafward movement of another.

We may pause here to contrast the vascular system of the plant with the circulatory system of a higher animal. Both animal and plant possess main channels for the transport of liquids to all parts of the body. There the analogy ceases. In such a vertebrate as man, a pumping mechanism, the heart, propels through a closed circuit a fluid medium carrying oxygen, food, and wastes. A circulatory system of this type may be compared with an endless belt, upon which various needed materials and waste products are continually deposited at different points and from which these substances are continually removed for use or disposal at various other points.

The transporting system of the plant, on the other hand, is composed of two independent units, each doing a different job and operating on a different principle and neither of them at all like the circulatory system of the animal. The *xylem* conduits form a unidirectional system of water transport, operating largely through transpiration pull—a mechanical process. The *phloem* channels are made up of the linked protoplasm of the phloem cells and through them, in either direction, move food and inorganic salts by diffusion or cell activity. Neither part of the vascular system is vitally concerned with respiration or excretion; oxygen and carbon dioxide are carried in solution in both, but the supply and elimination of these gases is accomplished for the most part by direct interchange with the atmosphere.

In addition to the primary functions of support and transportation, parts of the stem (particularly the phloem and parenchyma) may serve for temporary storage of manufactured food, water, or other substances. In many plants, also, the stem may play an important part in vegetative reproduction.

CHAPTER XIII

The Leaf and Its Functions

THE leaf is the food-manufacturing organ of the plant. Typically, it is a flattened structure, attached to a node of a stem, supported in such a way as to receive an optimum amount of sunlight, green in color because of the presence of great numbers of chlorophyll-containing cells.[1] Leaves are extremely varied in form and size, and their differences are among the conspicuous features that aid in recognizing the various kinds of plants. Nevertheless, most leaves are built on a common plan, which includes the following parts. There is a broad, flat, expanded portion, the *blade*, supported by a stalk, the *petiole*. Where the petiole is attached to the node, its base may be flanked by a pair of small leaflike appendages, the *stipules*. On both surfaces of the blade, there may be seen numerous *veins*, which are vascular bundles formed by repeated division of the large bundles that enter the blade from the petiole. The *venation*, or arrangement of the veins, forms a branching network in most dicotyledons, whereas in most monocotyledons, the veins run parallel, or approximately so.

The Structure of the Leaf. In cross section, the blade of a leaf is seen to consist of several layers. The upper and under surfaces are covered with a very thin *cuticle*—a noncellular layer composed of cutin, which is a waxlike, impermeable material secreted by the epidermal cells.[2] The presence of this coating greatly diminishes loss of water by evaporation. Just beneath the cuticle lies the *epidermis*, a single layer of cells that is continuous over the entire surface of the leaf. The upper surface is usually smoother than the lower, and one or both may be more or less densely covered with microscopic hairs. Small openings, the *stomata*, penetrate the cuticle and epidermis and communicate with air spaces within the leaf.

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[1] All functional leaves contain chlorophyll. If they do not appear green to the eye, it is either because of the presence of additional pigments that mask the green of the chlorophyll or because the surface is covered with light-reflecting hairs or is otherwise modified.

[2] A cutin layer covers all exposed surfaces of seedlings, herbaceous plants, and the young twigs of woody plants, as well as leaf surfaces.

The space between the two epidermal layers is filled, except where the veins occur, with parenchymous tissue, which is differentiated into two layers. The upper layer, one or two cells deep, is composed of tall, finger-shaped cells standing vertically beneath the epidermis. This is the *palisade parenchyma.* Its cells are closely packed together but with air spaces so arranged that each cell has at least one face in contact with the air. The palisade cells have a large central vacuole filled with cell sap, surrounded by a thin layer of protoplasm containing numerous small green plastids (*chloroplasts*), which contain chlorophyll. The lower and thicker layer of the parenchyma consists of a mass of thin-walled, loosely arranged cells, the *spongy parenchyma*, enclosing abundant air spaces that communicate with those of the palisade parenchyma. The cells of the spongy parenchyma also contain chloroplasts, though not nearly so many as the palisade cells.

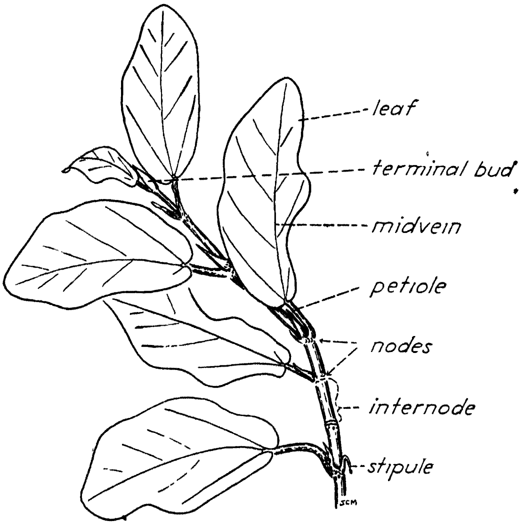


FIG. 64. *Stem and leaves of the climbing fig.*

The *stomata* are openings enclosed by a pair of specialized epidermal cells called *guard cells.* There are about 40 stomata per square millimeter on the upper surface of the bean leaf, compared to about 250 per square millimeter on the lower surface; and this ratio is quite typical of leaves in general. Under ordinary circumstances, the stomata open when light falls upon the leaf and close when light is withdrawn. This is brought about by increase in turgor of the guard cells when sugar manufacture begins under the influence of light and by decrease in turgor when photosynthesis ceases with darkness. The result is to permit free gaseous interchange with the atmosphere during those periods when active photosynthesis requires it. Because of this relation to sunlight, however, the stomata are relatively ineffectual in controlling evaporation. Concentration of stomata upon the lower surfaces of the leaves helps to reduce water loss, and devices to reduce air movement past the stomatal openings and thus lessen evaporation are common. Thus the stomata may open at the bottoms of deep pits or in a dense forest of minute hairs; or the leaf may be curled so that it will partly protect the lower surface from air currents.

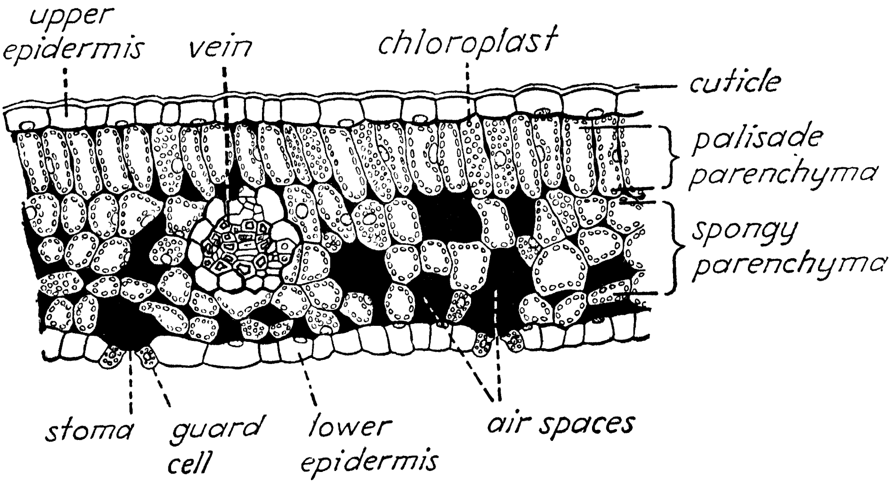


FIG. 65. *Cross section of a leaf, including a vein. (Courtesy of the General Biological Supply Company.)*

THE FUNCTIONING OF THE LEAF

The Food of Plants. The inorganic materials used by plants are commonly called *plant foods;* in popular usage, this term has become associated with fertilizers. It is, of course, a matter of definition as to what shall be regarded as a food. According to one commonly accepted definition, a food, whether used by animals or plants, is a substance which, either immediately or after a digestive process, may be oxidized to furnish energy or may be used in the building of protoplasm. By this definition, carbon dioxide, water, and the mineral constituents of the soil and of fertilizers can scarcely be classed as foods. The true foodstuffs are *carbohydrates, fats,* and *proteins* and possibly, by stretching a point, the *vitamins.* This definition of food has the advantage of emphasizing the fact that nutrition in plants and animals is an identical process. The two kinds of organism differ, not in the nature of the food that they use but in the *method of obtaining it.* We have already stressed the fact that the plant manufactures its food from inorganic substances, whereas the animal cannot do this and therefore must obtain its food directly or indirectly from the plant.

The Manufacture of Food by Photosynthesis. The basic food of the green plant is a simple sugar, generally *glucose,* from which are built up all the other carbohydrates, the fats, and the proteins used by plants. Glucose is produced by chemical combination of water and carbon dioxide. These two substances do not ordinarily react with one another; to make them do so requires the expenditure of energy and the presence of a catalyst. In the chloroplasts, water and carbon dioxide are brought together in the presence of the catalyst *chlorophyll* and are exposed to the action of light. Under these circumstances, the energy of the light breaks down the water and carbon dioxide, and through the catalytic action of the chlorophyll their atoms recombine to form glucose and free oxygen. This reaction is called *photosynthesis.* The complete reaction takes place according to the following equation:

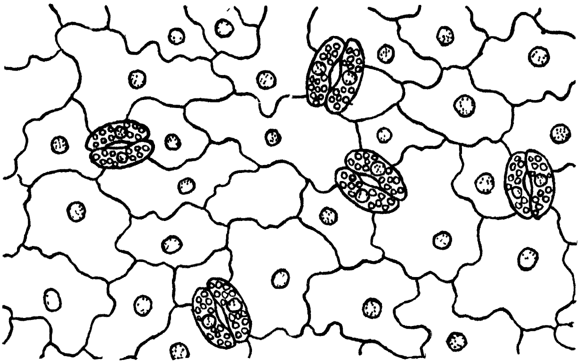


FIG. 66. *Portion of the lower epidermis, removed from a leaf of the privet, showing the stomata scattered among the ordinary cells (the latter having wavy outlines). (Courtesy of the General Biological Supply Company.)*

6 molecules of water	+	6 molecules of carbon dioxide	+	Light energy (through agency of chlorophyll)	(yields)	1 molecule of glucose	+	6 molecules of oxygen
$6H_2O$	+	$6CO_2$	+	Energy	→	$C_6H_{12}O_6$	+	$6O_2$

The actual chemical process, however, is much more complex than is here indicated, occurs in several steps that involve the temporary *formation of intermediate compounds, and is still very imperfectly understood.*

Any cell containing chlorophyll is capable of manufacturing glucose; but the greater part the work of photosynthesis is carried on by the parenchyma of the leaves. A leaf is an organ especially adapted for efficient utilization of the energy of light in the synthesis of glucose. The required water is brought from the roots through the xylem conduits. The carbon dioxide is almost wholly taken from the air through the stomata, though small amounts may be derived from the soil, and a part is released within the plant by oxidation of previously elaborated food. As the carbon dioxide is used up in the cells, that in the intercellular spaces diffuses into them, and additional quantities diffuse through the stomata into the air spaces.

The absorption area of the plant is so great that, although air contains only about 3 parts in 10,000 of carbon dioxide, relatively great quantities of this gas can be obtained from the atmosphere. Thus a moderately large oak tree may weigh, when dry, as much as 14,000 pounds. About 4 per cent of this dry weight consists of nitrogen and other materials derived from the soil, and about 60 per cent is hydrogen and oxygen. The remaining 36 per cent, or about 5,200 pounds, consists of carbon, originally taken in as carbon dioxide. This amount does not represent all the carbon dioxide that has entered the tree during its life, for oxidation of food and loss of the resulting carbon dioxide during the night must also be taken into account. But the remaining 5,200 pounds of carbon corresponds to the amount present in the carbon dioxide of 74 million cubic yards of air, which would fill a cube measuring about ¼ mile on a side. Proof that the great bulk of the carbon dioxide comes from the atmosphere and not from the soil is afforded by experiments in which plants are found to grow luxuriantly under conditions such that no dissolved carbon dioxide can be obtained by the roots.

In photosynthesis, two stable compounds are broken up, and an unstable one is formed. This involves the performance of work, in which the radiant *kinetic energy* of sunlight is transformed into *potential energy* stored in the form of glucose. Oxygen readily unites with glucose to restore the two original stable substances, water and carbon dioxide, and when this occurs, the energy that went into the making of the glucose is released. In the form of kinetic (now *chemical*) energy, it becomes available for the synthesis of glucose into other carbohydrates, fats, and proteins and for other forms of work. All life is made possible by the temporary storage and controlled release of energy, and since the sunlight-chlorophyll-glucose mechanism is the overwhelmingly predominant (thought not the only) device for energy capture, most living things are either directly or indirectly dependent upon it.

SOME FURTHER ASPECTS OF PLANT PHYSIOLOGY

The Relation Between Photosynthesis and Respiration. Respiration in plants and animals is identical; in both the process includes the intake of oxygen and the liberation of carbon dioxide. Each cell of an animal or plant body uses oxygen and produces carbon dioxide (and water) continuously, at a rate that varies with the activity of the cell. In the animal, the nature of respiration is plainly evident, since there is no other process requiring gaseous interchange with the environment. In the plant, on the other hand, there are two distinct processes that must be separately considered if confusion is to be avoided.

Respiration goes on continuously in the cells of the plant, using oxygen and producing carbon dioxide and water. At night, when photosynthesis is inoperative, respiration is the only factor in the situation, and at this time the leaf takes in oxygen and gives off carbon dioxide like an animal body. With the coming of day, the photosynthetic manufacture of glucose is resumed; but respiration also continues, if anything, at a faster rate than during the night. Since, however, photosynthesis requires such great quantities of carbon dioxide, the amount given off by respiration of the cells, although utilized, is altogether insufficient, and carbon dioxide from the outside begins to flow into the leaf. The cells continue to take in oxygen for their respiratory needs; but photosynthesis is producing it in such great quantities as a waste product that there is an oversupply within the leaf, and the excess that cannot be used in respiration diffuses out through the stomata.

It is often thought that because leaves take in carbon dioxide and give off oxygen during the day, respiration in plants is exactly the reverse of respiration in animals. In reality, it is identical in principle, and the day-night reversal of intake and outgo of the two gases results from overbalancing of respiration by photosynthesis during the day. The relations may be seen in the following tabular comparison of the two processes:

	Photosynthesis	*Respiration*
Place of occurrence . .	Only in chlorophyll-containing cells of green plants	In every living cell of both plants and animals
Time of occurrence . .	Only when the cells are illuminated	At all times during the life of the cell
Materials used.	Water and carbon dioxide	Oxygen (and fuel)
By-products	Oxygen	Water and carbon dioxide
Energy relations	Uses and stores energy	Releases energy
Effect on weight.	Body weight is increased	Body weight is decreased

Synthesis of Other Materials from Glucose. A part of the glucose produced by photosynthesis is directly used by the leaves and other parts of the plant, being oxidized with release of energy. A much larger portion is chemically transformed into a variety of other substances useful to the plant—food in forms suitable for storage; materials needed for building protoplasm and for forming the cell walls; enzymes; and other products. The majority of these syntheses are highly complex, and many of them are not or are but poorly understood; but we can gain some insight into the general nature of the changes that occur by considering a few of the simpler and more important cases.

As we have already seen, *glucose* (dextrose, grape sugar) is one of the simple sugars, or monosaccharides, with the chemical formula $C_6H_{12}O_6$. Plants also make another simple sugar, *fructose* (levulose, fruit sugar), which has the same chemical formula as glucose but somewhat different properties. Fructose, which is perhaps formed directly by photosynthesis like glucose, is still sweeter than the latter and is especially abundant in sweet fruits. It is thought to play a somewhat different part in plant metabolism than glucose, being more intimately connected with tissue formation, whereas glucose is primarily an energy food.

Most of the sugar stored in plants is in the form of *disaccharides*, or double sugars, which are made by the union of two monosaccharide molecules with the loss of one molecule of water, as shown by the following equation:

Glucose or fructose	+	Glucose or fructose	+	Energy	(yields)	a disaccharide	+	Water
$C_6H_{12}O_6$	+	$C_6H_{12}O_6$	+	Energy	→	$C_{12}H_{22}O_{11}$	+	H_2O

The two commonest disaccharides in plants are *sucrose* (cane sugar), composed of one molecule of glucose and one of fructose, and *maltose* (malt sugar), composed of two molecules of glucose. Sucrose is much the sweeter of the two and is the ordinary sugar that we use on the table. It is one of the commoner substances used by plants for food storage, and in plants like sugar cane and sugar beet, it almost wholly replaces starch in this role. Maltose is of interest, since it appears to be an intermediate step in the formation of the important material starch.

Starch is one of the chief food-storage materials; it is especially abundant in tubers, grains, and certain fruits and constitutes 30 to 70 per cent of the dry weight of our own food. Chemically, starch is a *polysaccharide, i.e.*, a carbohydrate built up of many monosaccharide units. It is related to maltose in somewhat the same way that maltose is related to glucose, since for each molecule of maltose that enters into the starch, one molecule of water is lost. The chemical formula of starch is $n(C_6H_{10}O_5)$, which, translated, means that the starch molecule is of no fixed size but contains an indefinite number (n) of the $C_6H_{10}O_5$ units; its structure is thought to be that of an indefinitely long chain of linked molecules, and the molecular weight is usually very high. Starch occurs in the form of granules; it is an excellent storage material, both because it is relatively insoluble, yet easily reconverted into soluble sugar for transportation, and because it contains more energy per unit of weight than do the sugars. During the day, granules of starch form in the chloroplasts where glucose is being made, the excess sugar being thus removed as fast as it is made and the sugar concentration prevented from becoming injuriously high. At night, these starch granules in the chloroplasts disappear, because of the reconversion of the starch into soluble sugars that are carried to other parts of the plant.

Cellulose is another polysaccharide formed from glucose. Although related chemically to starch, it is very much more insoluble and is highly resistant to chemical change. It is not affected by the ordinary digestive enzymes; animals such as ruminant mammals and termites, which use cellulose as food, are able to do so only through the presence in their digestive tracts of microorganisms capable of breaking down this substance. Fats, oils, and waxes are synthesized from sugars without the addition of any other elements; but the proportions of carbon, hydrogen, and oxygen in the molecule are changed, and the latter element is so greatly diminished in relative amount that the quantity of stored energy is very considerably increased. Fats and oils are extensively used by plants for food storage on account of this high energy content. In the synthesis of amino acids and proteins, carbohydrates are combined with nitrogen from the soil and sometimes also with sulphur, phosphorus, or other elements. The proteins thus formed constitute, with water, the bulk of the protoplasm of the cells; some of them are also stored as food (especially in the seeds of legumes) or are used in the making of enzymes and other cell products.

Enzyme Action in Plants. The chemical transformations that occur within the plant are nearly all brought about through the agency of various enzymes. We have already seen something of the nature and functioning of these organic catalysts in our study of the human body, and it will be recalled that one of their characteristics is a high degree of specificity in the substances upon which they act. Each enzyme affects only a single chemical reaction. In view of the multiplicity of the chemical reactions that occur within the plant cell, it would therefore seem that each cell must either be equipped with a battery of enzymes or else be able to produce any given enzyme at need. Some of the enzyme-controlled reactions are reversible, the direction of the reaction being controlled by the relative concentrations of the substances taking part; thus, under experimental conditions, *lipase*, found in plants as well as in animals, in the presence of excess fat splits the fat into glycerol and fatty acids, but in the presence of excess glycerol and fatty acids causes these to combine into fat. The plant cells are apparently able to control the direction of this process by the expenditure of energy. Most enzyme-controlled reactions, however, are in practice unidirectional; thus some enzymes build up a complex substance from simpler ones with the expenditure of energy (synthesis), whereas others break down a complex substance into simpler ones with liberation of energy.

As a concrete example of enzyme activity in plants, we may consider the process by which starch is split up into monosaccharide molecules. Starch being so nearly insoluble, its conversion into soluble form may be regarded as a kind of intracellular digestion comparable to the digestive process in animals. The splitting is accomplished by two specific enzymes. The first of these, *diastase*, changes starch back to the sugar, maltose, by the addition of $n/2$ molecules of water to each starch molecule $n(C_6H_{10}O_5)$, as shown by the following equation, in which we may take n as equal to 200:

Starch molecule	+	Water molecules	(yields)	Maltose molecules	+	Energy
$200(C_6H_{10}O_5)$	+	$100H_2O$	$\rightarrow$	$100C_{12}H_{22}O_{11}$	+	Energy
		(in the presence of diastase)				

As soon as this reaction has taken place, the maltose is generally converted into glucose by the action of the second enzyme, *maltase*, as shown by the equation

Maltose molecule	+	Water molecule	(yields)	Glucose molecules	+	Energy
$C_{12}H_{22}O_{11}$	+	H_2O	$\rightarrow$	$2C_6H_{12}O_6$	+	Energy
		(in the presence of maltase)				

This particular kind of molecule splitting is called *hydrolysis*—the union of a complex compound with water accompanied by its breaking up into less complex compounds. The process outlined above is just the reverse of that by which the glucose was synthesized into starch.

The enzyme diastase is similar to and perhaps identical with the ptyalin of human saliva. Maltase of plants is the same enzyme as that found in the small intestine of man, where it breaks down maltose sugar just as it does in the plant cell. Some of the other enzymes present in plants are *invertase*, splitting cane sugar into glucose and fructose, and found also in the small intestine of man; *cellulase*, changing cellulose to glucose, and not present in vertebrates; *lipase*, mentioned above as an example of enzymes with reversible action, changing fats to fatty acids and glycerin or vice versa, and found also in the human stomach. Various *proteinases* that convert proteins to amino acids by a series of steps, much as pepsin and trypsin work together in man, are also present.

CHAPTER XIV

Flowers and Fruits

In describing the structure and functioning of the individual animal, as exemplified by man, we found it necessary to include in our account certain aspects of the reproductive system, in spite of the fact that this system has primarily to do with the maintenance of the race rather than of the individual. Similarly, in dealing with the individual plant, we can scarcely omit some consideration of those reproductive structures so characteristic of all higher plants—the flower and the fruit. Their role in plant reproduction is the theme of a later chapter; here we shall direct our attention chiefly to the structure of flowers and fruits and their relations to the rest of the plant body.

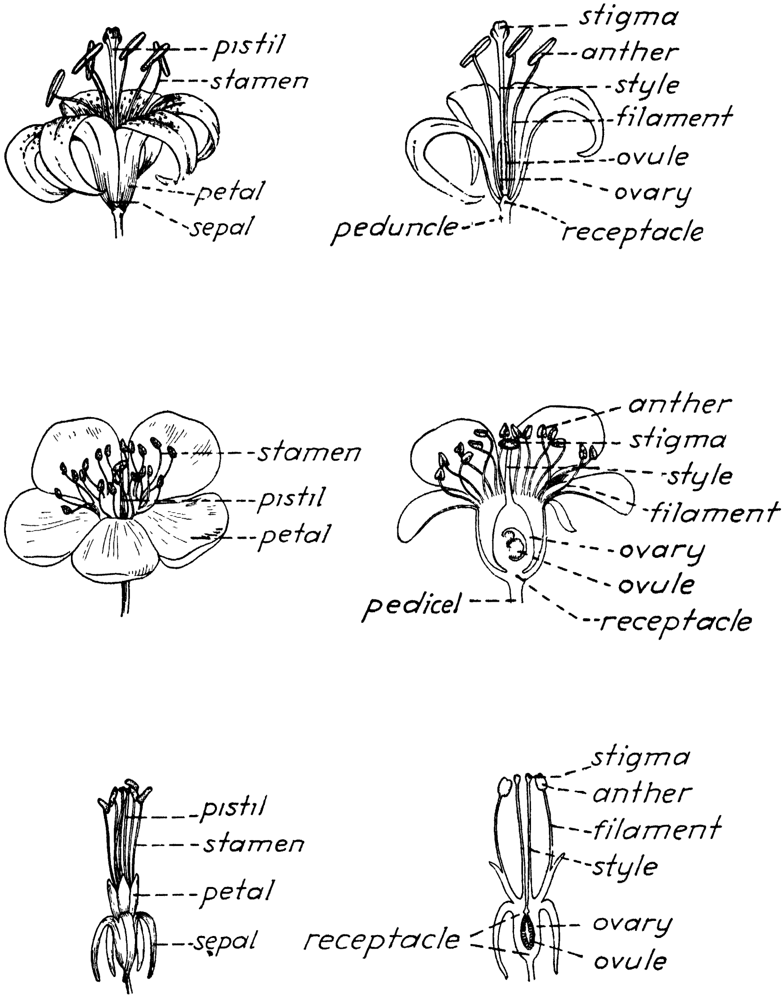
The ***flower*** is a special reproductive structure confined to and characteristic of the members of the highest plant phylum, the angiosperms. The terms *angiosperm* and *flowering plant* are synonymous. Essentially, the flower consists of an assemblage of parts derived from leaves, all more or less highly modified, borne upon a modified twig, and concerned with the production of the seed.

The modified branch that bears the flowers arises from a bud situated in the axil of a leaf, like an ordinary foliage branch. The leaf at the base of the flower branch, however, is not usually of the same form as the foliage leaves; it is called a *bract*. It is usually small and often deciduous but sometimes enlarges to enclose the flower or takes part in its formation. The flower-bearing axis may be either branched or unbranched. When unbranched it bears a single flower at its apex and is called a *peduncle*. Often, however, the axis is branched and the flowers are borne in clusters or inflorescences. In this event the usually short stems of the individual flowers are called *pedicels*, and the term peduncle is applied to the main stem of the entire flower cluster. A peduncle is thus the stem of a solitary flower or of an inflorescence, while a pedicel is the individual stem of a flower that is a part of a cluster. The flower-bearing branch differs from an ordinary foliage branch in important respects. It is often without recognizable leaves, though it may have green bracts at the bases of the peduncles or pedicels. Most of its "leaves" have been transformed into the flower parts, densely crowded together at the twig apex and not separated by distinct internodes, as in foliage branches. Lastly, in a flower-bearing branch, the meristem is entirely used up in making the floral leaves, instead of forming a persistent growing point, as in an ordinary branch.

The Structure of a Typical Flower. The parts that make up the flower may be divided into essential and accessory structures. The essential parts are the *sporophylls*, which produce the male and female sex cells. The male sporophylls, in which pollen grains develop, are the *stamens*, each consisting of a *filament*, or stalk, supporting an *anther*, or pollen-producing organ. Each stamen consists of a single male sporophyll. The female structures are the *pistils*. Each consists of a basal part, the *ovary*, in which the egg cells or ovules develop and which takes part in the formation of the fruit; a *style* projecting from the ovary, through which the pollen tube grows to effect fertilization after pollination has occurred; and a *stigma*, or expanded tip of the style, to which the pollen adheres. A pistil may consist of a single female sporophyll (*carpel*), in which case the ovary has a single chamber; more often it consists of several fused carpels, and the ovary contains an equivalent number of ovule-bearing areas (*placentae*) in separate chambers or in a single chamber produced by fusion of the carpels.

The accessory parts of the flower are the *petals* (collectively called the *corolla*), often large and brightly colored, forming one or more rings outside the stamens; the *sepals* (collectively called the *calyx*), usually smaller than the petals, often green in color, enclosing the base of the petals; the *receptacle*, or expanded tip of the flower stalk to which the sepals, petals, stamens, and pistils are attached; and the peduncle or pedicel, which forms the immediate stalk of the flower. This stalk and the receptacle are parts of the axis of the plant; all the remaining parts are modified leaves. In most flowers, the pistils stand at the center; the remaining parts are arranged in a spiral or in concentric rings around the pistils—first one or more rows of stamens, then the petals, and on the outside, the calyx whorl.

Modifications in Flower Structure. Within the limitations imposed by this scheme, flowers show innumerable variations in structure, arrangement, and appearance. They may be large and brightly colored or small and inconspicuous; they may be composed of a large number of parts or of relatively few; they may possess both stamens and pistils or only one or the other; petals and sepals may be present, or one or both of these sets of accessory structures may be lacking. Flowers that possess both male and female organs are said to be *perfect;* those that lack stamens or pistils are said to be *imperfect.* Perfect flowers with both petals and sepals are *complete;* but if any one of the sets of flower parts is missing, the flower is *incomplete.* Hence, if either petals or sepals are absent, the flower is incomplete, though it may be perfect; but if either stamens or pistils are missing, the flower is necessarily both incomplete and imperfect.


pistil
stamen
petal
sepal
stigma
anther
style
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ovule
ovary
peduncle
receptacle
stamen
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anther
stigma
style
filament
ovary
ovule
pedicel
receptacle
pistil
stamen
petal
sepal
stigma
anther
filament
style
receptacle
ovary
ovule

FIG. 67. *Some types and structures of flowers. (Courtesy of the General Biological Supply Company.)*

The number, arrangement, and form of the flower parts vary much from group to group of the angiosperms and furnish the best characters for their classification. The parts may be arranged in a *spiral,* or in the much more frequent pattern of concentric circles called the *cycle* arrangement. All the petals and all the sepals may be alike, in which case the flower is *regular*, like that of a lily or a wild plum; or some of the petals or sepals may be much larger or may be differently shaped than the others, making the flower *irregular*, like that of the sweet pea. Often the individual parts of one whorl or circle become fused together or fused with the parts of adjacent whorls. Thus several carpels may fuse to form a compound ovary, or the stamens may join into a solid ring, or the petals may unite into a tubular structure. Frequently the stamens appear to arise from the inner surface of a tubular corolla, their bases having fused with those of the petals. The pistil may be attached to the receptacle merely at the base, so that the ovary is exposed and is said to be *superior;* or the sides of the receptacle may grow up around the ovary and fuse with its walls, in which case the ovary is said to be *inferior.*

Arrangement. Besides the differences that exist in the flowers themselves, their arrangement on the axis (*inflorescence*) varies greatly from plant to plant. Sometimes a single flower is borne at the end of the unbranched peduncle. Often the peduncle does not produce a flower at its tip but sends off lateral pedicels, each bearing a flower. If the pedicels and peduncle are both long, this makes a loose cluster of flowers called a *raceme*, as in wild plum; if the pedicels are very short or if the flowers are sessile, we have a *spike*, as in plantain, or various modified types of spikes, such as the spikelet of grasses, the catkin of willows, the spadix of white arum and Jack-in-the-pulpit, and the scaly strobilus of hops.

When, in this type of inflorescence, the branching is continued, various types of compound racemes and spikes are produced; one very common form is the globular flower cluster of the Umbelliferae, in which the axis is very short and the branches and pedicels are long and radiating. Another common type of flower arrangement is the cyme, produced when the central axis terminates in a flower but sends off side branches, which themselves end in flowers; these may continue the branching process, giving rise to compound cymes.

Finally, we have in one very large group of plants, the *composites* (of which daisies and sunflowers are examples), flower clusters consisting of dozens or hundreds of small individual flowers borne crowded together on the surface of a greatly enlarged and conical or flattened receptacle. The structure popularly regarded as a flower in this group is really a very dense mass of flowers, called a *head.* In such heads, the small individual flowers are often of two sorts—those in the center (the *disk flowers*) perfect, with inconspicuous corollas; and those around the margin (the *ray flowers*) imperfect and sterile, the tubular corolla of each forming a conspicuous strap-shaped projection or ray, which resembles a single petal of an ordinary flower.

Monoecious and Dioecious Conditions All plants that possess perfect flowers are hermaphroditic and are said to be *monoecious*,[1] since male and female sex cells are both produced by the same plant. In plants that have imperfect flowers, the *staminate* (male) flowers and the *pistillate* (female) flowers may occur on the same plant (as in corn, oak, and maple), in which case the plant as a whole is still monoecious. More rarely, the staminate and pistillate flowers may be confined to different individual plants of the same species (as in the date palm, papaya, holly, and willow). In this event, the species is said to be *dioecious*,[1] since the male and female sex cells occur in separate individuals.

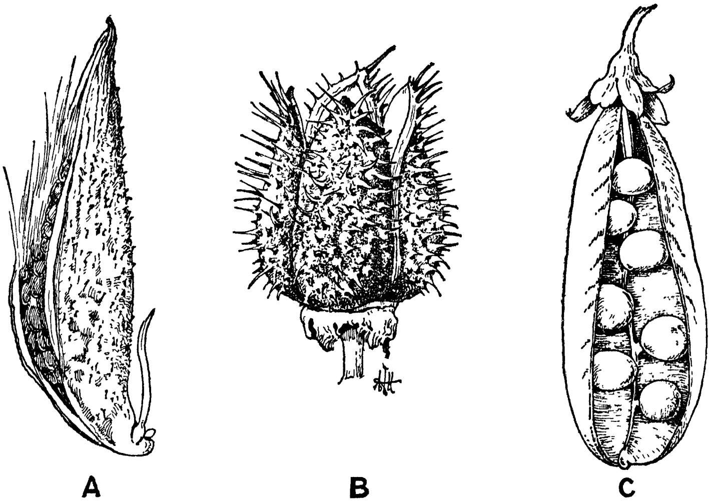

FIG. 68. *Dry fruits: (A) follicle of common milkweed; (B) capsule of Jimson weed; (C) legume of garden pea. (From Haupt, An Introduction to Botany.)*

Seeds and Fruits. As a result of the fertilization of the ovule by a pollen grain, as will be discussed later, the ovule begins to develop into an embryonic plant within the ovary. The petals fall, and the style, stigma, and stamens of the flower wither away. The ovary, however, enlarges with the growth of the young plant within it; the latter becomes a seed, enclosed in hard seed coats formed from the walls of the ovule. The matured ovary, enclosing its one or more seeds, together with any other parts of the flower (usually the receptacle) that have shared in the postfertilization growth and maturation of the ovary, form the reproductive structure known as a *fruit*. The term is here used in its technical sense, which is more comprehensive than the popular one. The definition of a fruit given above would include such one-seeded dry fruits as corn, oats, wheat, and other cereal grains that are commonly spoken of as "seeds," in addition to tomatoes, the pods of beans and peas, nuts such as walnuts and acorns, and many other structures that are not fruits in the popular sense.

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[1] Words derived from the Greek *oikos*, "house or dwelling place." *Mon*-oecious plants have the male and female sex cells "in one house"; *di*-oecious plants have them separated, "in two houses."

According to whether the ovary was formed from a single carpel or from two or more fused carpels, the fruit may contain one, two, or more seed-producing areas, in one or more seed-chambers. The matured ovary wall may remain thin, or it may thicken greatly; as a whole, it is known as the *pericarp.* In many fruits, it differentiates into three layers—an outer skin, or *exocarp;* a more or less thickened middle portion, or *mesocarp;* and an inner layer, the *endocarp.* In the stone fruits, such as the peach, the mesocarp is fleshy, and the endocarp forms a stony wall about the seed; in "nuts," such as the pecan, the mesocarp is a woody husk surrounding a hard endocarp that forms the "shell"; in the apple, the mesocarp is fleshy and the endocarp thin and papery, forming the "core." Not all the flesh of the apple is mesocarp, however; in some fruits, including the apple and strawberry, the receptacle enlarges and shares in forming the fruit. The most important types of fruits may be classified as follows[1]:

I. *Simple fruits*, consisting of a single enlarged ovary, with which some other flower parts may be incorporated. Most of the common fruits, except those listed below under *B* and *C*, are simple fruits.
  - *A*. *Fleshy fruits* (ovary wall fleshy, at least in part, or until maturity).
    1. *Berry*—the ovary wall fleshy, enclosing one or more seeds Examples: grape, gooseberry, currant, pepper, persimmon, tomato, banana, date (the "stone" of the last being a seed).
       As special types of berries we have:
       - *a*. *Pepo*—a type of berry with hard rind composed largely of the receptacle. Examples: squash, cucumber, cantaloupe, watermelon.
       - *b*. *Hesperidium*—a type of berry with leathery, oily rind, and juicy pulp composed of numerous "cells." Examples: orange, grapefruit, lemon.
    2. *Drupe or "stone" fruits*—one-seeded, the seed enclosed in a "stone" or "pit" made up of the stony endocarp; mesocarp fleshy, exocarp thin, forming the skin. Examples: cherry, peach, mango, plum, olive. Such "nuts" as almond, walnut and pecan also belong here; the almond is the stone of a typical drupe, and the shell of walnuts and pecans is the stone of a drupe, the fleshy part of which is represented by the husk.
    3. *Pome*—outer part of the ovary wall fleshy and enclosed in the fleshy receptacle; inner part of ovary wall papery, forming the "core." Examples: pear, apple, quince.
  - *B*. *Dry fruits* (ovary wall dry).
    1. *Dehiscent fruits* (splitting open when ripe).
       - *a*. *Legume* or true pod—ovary composed of a single, modified, seed-bearing leaf (carpel), seeds attached along one side; splitting along two sutures when ripe. Examples: pea, bean, vetch.

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[1] Reprinted by permission, with modifications, from Holman and Robbins, "Textbook of General Botany," published by John Wiley and Sons, Inc.

  - *b. Follicle*—ovary composed of one carpel; splitting along only one suture when ripe. Examples: milkweed, larkspur, columbine, peony.
  - *c. Capsule*—ovary composed of two or more carpels; opening when ripe in one of three ways—along the line of junction of the carpels (azalea), along the middle of each carpel (iris, lily), or by pores (poppy).
  - *d. Silique*—ovary composed of two carpels, the sides of which split off at maturity, leaving a persistent middle partition. Examples: mustard, cabbage, turnip, radish, cauliflower.
- 2. *Indehiscent fruits* (not splitting open when ripe).
  - *a. Achene*—one-seeded, the seed attached to the ovary wall at only one point. Examples: buckwheat, sunflower, buttercup, ragweed.
  - *b. Caryopsis*, or "grain"—one-seeded, the seed firmly united to the seed coat on all sides. *Examples:* Wheat, corn, rice, barley, broom corn, oats, and all other grasses.
  - *c. Samara*, or "winged" fruits—one or two-seeded, the ovary wall forming a winglike outgrowth that extends about the seed. Examples: ash, elm, maple.
  - *d. Schizocarp*—carpels two or more, united during growth, splitting apart but not opening at maturity. Examples: carrot, parsnip, parsley, celery, mallow.
  - *e. Nut*—a hard, one-seeded fruit, generally resulting from a compound ovary. Examples: acorn, chestnut, hazelnut. Many so-called "nuts" are seeds; others are achenes or the stones of drupes (see I, *A*, 2, above).

II. *Aggregate fruits*, consisting of a number of enlarged ovaries, belonging to a single flower and massed on or scattered over the surface of a single receptacle. The separate ovaries are spoken of as *fruitlets*. Examples: raspberry (the fruitlets are drupes and separate easily from the receptacle); blackberry (drupes, closely attached to the receptacle); strawberry (achenes, on a fleshy receptacle that constitutes most of the edible portion of the fruit); magnolia (conelike masses of follicles).

III. *Multiple fruits*, consisting of the enlarged ovaries of several or many flowers more or less coalesced into one mass. Examples: mulberry (achenes, each surrounded by a fleshy, juicy calyx); fig (achenes, on the inner surface of an enlarged hollow receptacle); pineapple (axial stem, with the fleshy receptacles and ovaries of many sessile flowers fused together); sweet gum (many partly fused capsules).

CHAPTER XV

Some Other Types of Individual Organization

Variety of Structure versus Uniformity of Function

One needs only to look about him to see something of the extraordinary variety of size, form, and structure that exist among organisms; and when the world revealed by the microscope is also considered, the diversity of living things proves to be very great indeed. Considerably more than 1 million kinds of animals and plants are known today, and additional ones are constantly being discovered. Out of this vast assemblage, we have examined two types in some detail—man, to illustrate the problems of individual structure and functioning among animals, and a flowering plant, to show how these problems are met by a member of the plant kingdom. Our survey of these has now been completed; but a question that still confronts us is to what extent these selected examples are representative of other organisms. In briefly considering this question, we shall also, in a sense, be summarizing the essential features of individual organization and functioning, freed from much specific detail that has necessarily been included in our treatment of man and the higher plants.

The thesis of this chapter is that, no matter what their size, form, or structure, *all individual organisms encounter the same basic problems of living but solve these problems in unlike ways.* The number of different ways of doing the necessary tasks and of types of organization associated with these methods is not, however, so great as might be supposed. We have already seen that the most basic divergence among organisms lies in the means by which the problem of nutrition has been met. The plant has adopted one method, the animal another, and the consequences are so far-reaching that we shall have to examine the chief patterns of animal and of plant life separately and by somewhat different treatments.

THE VARIED PATTERNS OF ANIMAL LIFE

If we ignore all except the most striking and fundamental differences among animals, we can group the more than three-quarter million known kinds into a few major assemblages, based on different degrees of complexity in organization and the extent of "division of labor" among the parts of the individual. We shall first briefly examine four different levels of construction found among animals and then see how the common tasks of life are performed at each of these levels.

Structural Levels

In one large group of animals, the Protozoa,[1] each individual consists of a single cell.[2] This one cell must perform all the functions essential for animal life—capture its own food and digest it, carry on respiration, excrete metabolic wastes, respond appropriately to the stimuli from its environment, and reproduce its kind. Such a single-celled animal lives on what we may call the *protoplasmic level of construction*. Such organization as it shows for the performance of various functions is confined to the protoplasm of the cell itself. The Protozoa lack tissues and organs and

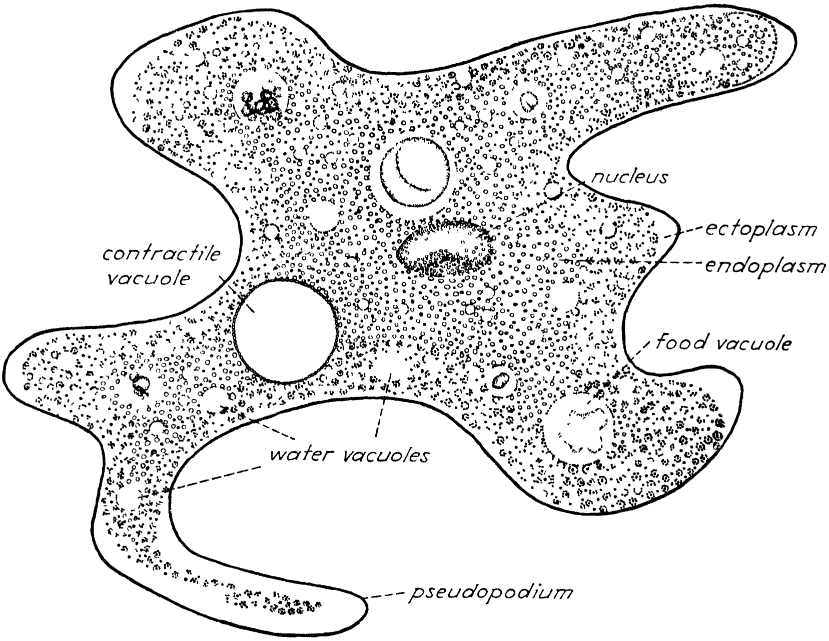

FIG. 69. *Amoeba, a simple protozoan. Compare with the drawing of a single metazoan cell, Fig. 4.*

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[1] The animal groups mentioned in this chapter are defined and illustrated in Appendix A.

[2] Some protozoa are colonial; *i.e.*, a number of individual cells are bound together mechanically to form a several- or many-celled unit. Such a *colony* can be distinguished from a multicellular individual by the fact that the cells composing it are all alike and are physiologically independent of one another.

do not have any very complex structures correlated with particular functions. Nevertheless, they should not be thought of as simple; no cell is simple, and these separate-living cells have to do many more things than the specialized cells of the human body and are correspondingly complicated. Amoeba is an excellent example of these unspecialized, single-celled animals.

In more than 90 per cent of all known kinds of animals, the individual is made up of at least many hundreds and often of billions of cells. The many cells that compose the body exhibit a greater or less amount of differentiation and specialization for particular tasks, and in all but the simplest types are organized into tissues, into tissues and organs, or into tissues, organs and systems.

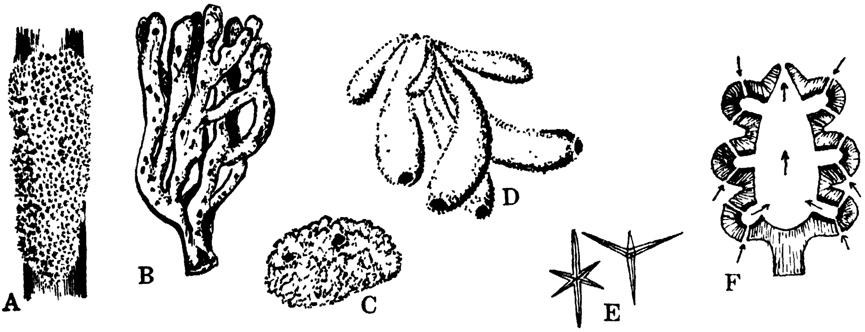

FIG. 70. *Sponges. (A–D) Some common types; (E) spicules of a calcareous sponge; (F) a diagrammatic section of a simple sponge illustrating the canal system and the two layers of cells; arrows indicate the direction of the flow of water*

Of these many-celled animals (often collectively called the Metazoa), the *sponges* are the simplest and least highly organized. The ordinary bath sponge, to use a well-known example, is a loose aggregation of semi-independent cells, but none of these cells must or can, like the protozoan, perform *all* the tasks of maintenance. Instead, the cells have become somewhat differentiated and show some division of labor and a degree of cooperation. These differentiated cells are not, however, organized into definite tissues, and the sponge has no organs or means of coordination other than a simple mechanical relationship between the cells. The body functions are carried on by the cells acting as units, and the whole sponge functions at what may be called the *cellular level of construction.*

The simplest animals in which specialized cells are organized into definite tissues are coelenterates—a group to which Hydra, jellyfishes, and corals belong. This grouping of similar cells brings increased efficiency, since the cells are enabled to act in a more coordinated fashion and with massed effect. The coelenterates may be said to have reached the *tissue level of construction.* The small, threadlike, many-armed fresh-water animal known as Hydra is a good example of the group. It is saclike in construction, the body wall being made up of two layers of cells surrounding a digestive cavity; this cavity is the only one in the body and has but one opening, the mouth.

A step in advance of the coelenterate type of structure is shown by the small, free-living flatworm, Planaria, in which definite organs are present. This worm resembles Hydra in having only a single cavity in the body, with a single opening, the mouth. However, in addition to the two cell layers corresponding to those that form the body wall in Hydra, there is present in Planaria a third layer between them, which makes up most of the bulk of the body and takes part in the formation of various organs. Among the simple organs of Planaria are a muscular pharynx for ingesting food, nerve cords and light-sensitive eyespots, excretory apparatus, and reproductive organs. Even in this lowly worm, there is a suggestion of organ systems in the arrangement of the digestive, excretory, and nervous structures.

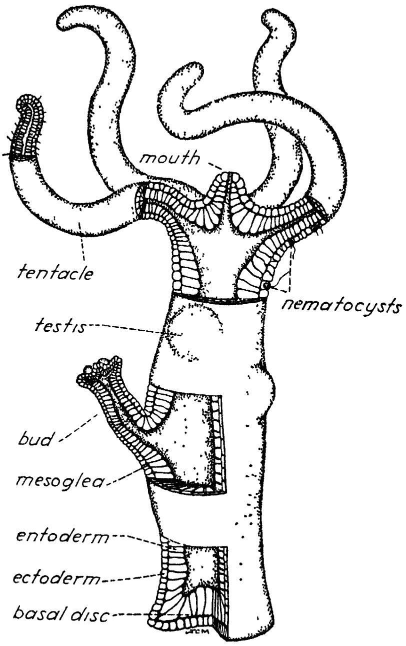

FIG. 71. *A diagrammatic longitudinal section of Hydra, a simple metazoan on the tissue level of organization.*

Above the plane of the flatworms, nearly all the Metazoa have attained the *organ-system level of construction.* In these higher Metazoa, we not only find cells functioning individually, cell groups working together as tissues, and tissues cooperating in the formation of organs—the organs themselves are, for the most part, grouped into systems, each system being adapted for the performance of one or a few functions. The human body is constructed on this plan, and in Chap. II, its hierarchy of cells, tissues, organs, and systems was described. Animals whose organization has attained this level share certain fundamental characteristics in spite of their many differences. In all of them, the bulk of the body is formed from the third cell layer (mesoderm), which we first noted in the flatworms. They all have a body space surrounding the digestive tract, so that the plan of the body is essentially that of a tube within a tube. Further than this it becomes difficult to generalize, because the structural patterns of the higher Metazoa have diverged along a number of quite distinct lines, related to different modes of development, habitat, and ways of life. All, however, have attained more or less high degrees of organization and integration. Most of the higher Metazoa are comparatively bulky; nearly all have some type of circulatory system; and the nervous system and sense organs are much more complex and highly developed than in the lower types, permitting adaptation to more varied and complicated environments. Many of these higher Metazoa are specialized for a wholly terrestrial existence. Insects, spiders, crabs,

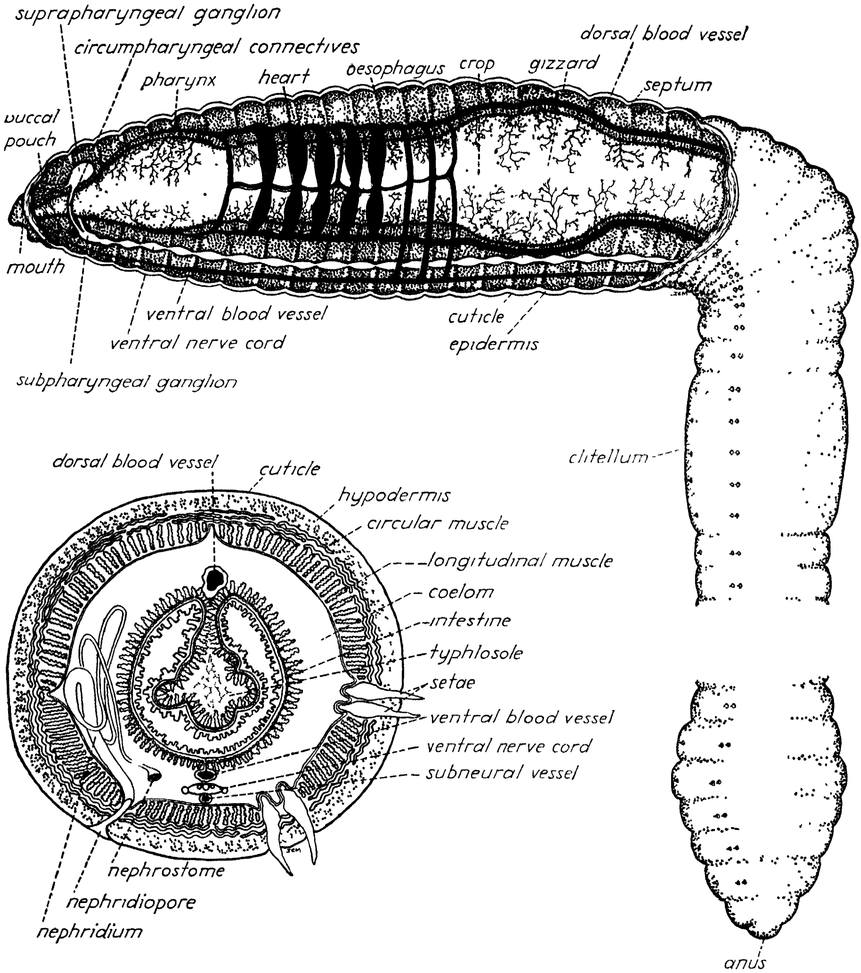
suprapharyngeal ganglion
circumpharyngeal connectives
pharynx
heart
oesophagus
crop
gizzard
dorsal blood vessel
septum
buccal pouch
mouth
ventral blood vessel
ventral nerve cord
subpharyngeal ganglion
cuticle
epidermis
clitellum
dorsal blood vessel
cuticle
hypodermis
circular muscle
longitudinal muscle
coelom
intestine
typhlosole
setae
ventral blood vessel
ventral nerve cord
subneural vessel
nephrostome
nephridiopore
nephridium
anus

FIG. 72. *A longitudinal and a cross section of an earthworm, an animal on the organ-system level of organization. The reproductive systems (male and female) have been omitted. (Courtesy of the General Biological Supply Company.)*

worms, starfishes, clams, snails, and the vertebrates (fishes, frogs, reptiles, birds, and mammals) are examples of Metazoa built on the organ-system plan. From among these, the *earthworm*, the *grasshopper*, and *man* may be selected as examples to illustrate relatively simple, moderately complex, and highly complex types of structure at this organizational level.

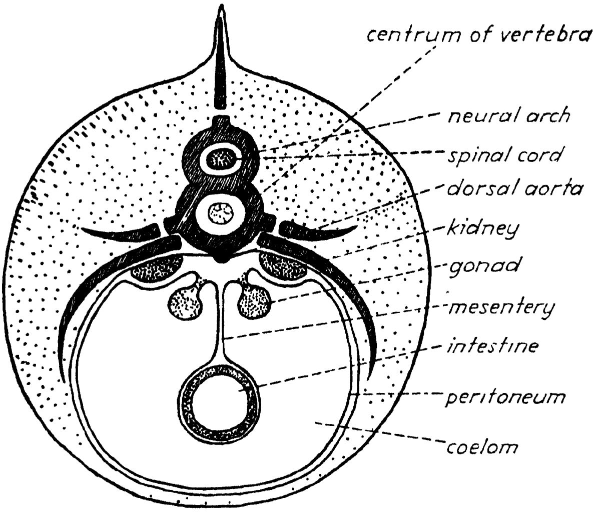

FIG. 73. *A cross section of a diagrammatic lower vertebrate to illustrate a highly specialized organ-system construction.*

DIFFERENT WAYS OF DOING THE SAME THINGS

We shall now see how some animals representative of different levels of construction carry on some of the fundamental processes necessary for life. For our purposes, it will be sufficient to consider digestion, respiration, excretion, and the response to stimuli. The various reproductive methods and breeding habits associated with the different organizational levels will be presented in Chap. XVII.

Digestion

The purpose of digestion is the same in all animals—*i.e.*, to break down foodstuffs into a form in which they can be taken into the protoplasm of the cell. According to whether this is done by individual cells or by cells acting in concert, digestive methods can be classified under two heads.

Intracellular Digestion. In the Protozoa and the sponges, digestion takes place within the individual cells. Food particles are taken into temporarily formed, liquid-filled spaces surrounded by protoplasm and protoplasm, diffuse into the vacuoles and digest the food particles; the products of digestion then diffuse into the protoplasm. Indigestible residues are eliminated from the cell through the cell membrane by a "bursting" of the vacuoles to the outside.

Extracellular Digestion. In all the more complex animals, digestion takes place in a *body cavity surrounded by digestive cells.* Both intra- and extracellular digestion occur in some of the simple metazoa, such as Hydra. All extracellular digestion requires a digestive organ or organ system. The chief types of digestive structures are:

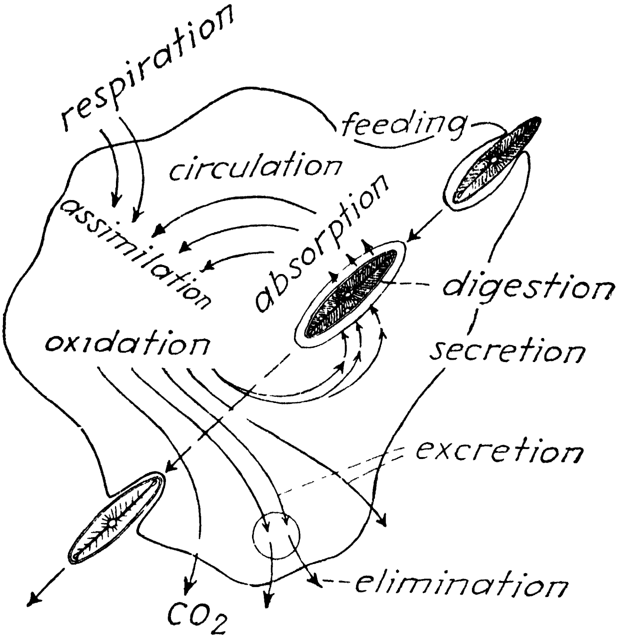

FIG. 74. *Diagram showing the steps in metabolism in Amoeba. Compare with Fig. 8, which is a similar diagram of the same processes in man. (From Wolcott, Animal Biology.)*

1. *The Coelenteron.* A digestive sac, found in very simple metazoa; it has but one opening, the mouth. In the flatworms, the coelenteron is highly branched and ramifies throughout the body so that all other tissues are within absorbing distance of the digested food.

2. *The Enteron.* In all groups more complex than the flatworms, the coelenteron, as a digestive cavity, is supplanted by a structure known as the *enteron,* a digestive tube open at both ends, *i.e.,* having both a mouth and an anus.

Digestion in the Earthworm. The enteron of the earthworm may be used as an example of a digestive tube that has been differentiated to form a system of organs. It consists of a *mouth,* opening into a ***buccal cavity,*** a *pharynx* with strong muscular walls, an *esophagus,* a ***crop*** in which food accumulates, a *gizzard* with thick muscular walls and a hard lining by means of which food may be finely ground, an *intestine* with secreting and absorptive cells, and an *anus.* An internal ridge, the typhlosole, formed by an infolding of the dorsal wall of the intestine, gives increased surface. The exterior surface of the intestine is covered by a layer of brown chloragogen cells, which appears to function as a digestive gland.

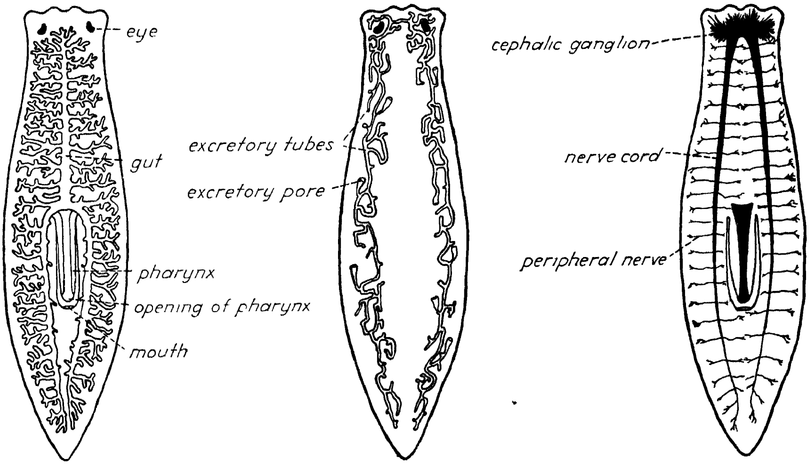

FIG. 75 *Three diagrams of the fresh-water flatworm Planaria. (A) Digestive system; (B) the excretory system; (C) the nervous system. (From Parker and Haswell, Textbook of Zoology, The Macmillan Company.)*

Digestive Systems in the Vertebrates. In the vertebrates, the digestive system reaches its highest development. Here it not only consists of an alimentary canal, subdivided into regions, but also possesses highly developed glands which produce digestive secretions. This type has already been studied in man.

Modifications. Although primarily for digestion, certain parts of the enteron may be used for other purposes in some groups of animals. Thus, in the sea cucumbers and in certain groups of aquatic insects, the rectum is secondarily used as a respiratory organ; and in all insects, excretion is carried on by numerous fine tubules opening into the posterior part of the enteron.

Respiration

All animals are dependent upon the oxidation of foodstuffs for energy and so have a continual need for oxygen and for the elimination of carbon dioxide. The quantities of oxygen required, and of carbon dioxide that must be eliminated are proportional to the amount of protoplasm and the rate of metabolism. When the animal is very small, the ratio of its body surface to the volume of its protoplasm is comparatively great, and if the surface is permeable to oxygen and carbon dioxide, it may be sufficient to meet all respiratory needs. Several factors, however, set a limit to the utilization of the body surface as a respiratory membrane. As the size of the body increases, two distinct types of respiratory complications result: (1) the *ratio of body surface to volume* decreases and becomes inadequate for a sufficient respiratory exchange; (2) a high proportion of body tissues are now *internal*, with no direct access to the external medium. Any increase in the metabolic rate will, of course, increase the minimum ratio of surface to volume necessary for an adequate respiratory exchange; and the various adaptations of body surfaces for protection against mechanical injury or loss of water decrease or wholly destroy their properties as respiratory membranes. All but the simplest and smallest metazoans have consequently had to develop special respiratory processes and structures.

Types of Respiratory Processes. Four more or less distinct types of respiratory processes can be distinguished. *Simple respiration* involves a direct exchange through the cell membrane between the protoplasm of the cell and the gases of the external medium. When a circulating medium (blood) is utilized to provide for the respiratory needs of internal tissues, respiration involves two distinct processes: *external respiration*, in which the blood makes a gaseous exchange with the external medium; and *internal respiration*, in which a gaseous interchange takes place between the aerated blood and the protoplasm of the cells. Finally, in many organisms, the necessity of providing special respiratory surfaces (which in most instances must be protected against loss of water, mechanical injury, or both) is associated with *breathing*, a process that results in the continual aeration of the respiratory surface.

Simple Direct Respiration. The simplest of all respiratory processes is found in the Protozoa, the lowest Metazoa, and in certain minute representatives of the intermediate and higher Metazoa. Here, since the ratio of surface to volume is large, since all protoplasm is within a very short distance of the body surface, and since the latter is freely permeable to oxygen and carbon dioxide, an adequate gaseous exchange is provided by a direct diffusion between the protoplasm and the external medium.

The Direct Respiration of Insects. A far more complicated type of direct respiration has been developed by the insects and certain of their relatives. Here the tough exoskeleton and the comparatively huge proportion of internal tissues preclude gaseous interchange through the body surface, and there has been developed a complex network of ramifying air tubes (tracheae), that lead from external openings to all of the tissues. At their ultimate branches the tracheae communicate with numerous very fine, thin-walled, liquid-filled tubules, the *tracheoles*, in which by diffusion oxygen is carried to and carbon dioxide from the immediate vicinity of the cells. Since these tubes and tubules are internal and comprise a tremendous total linear extent, regular muscular breathing movements are required to bring about the necessary renewal of fresh air.

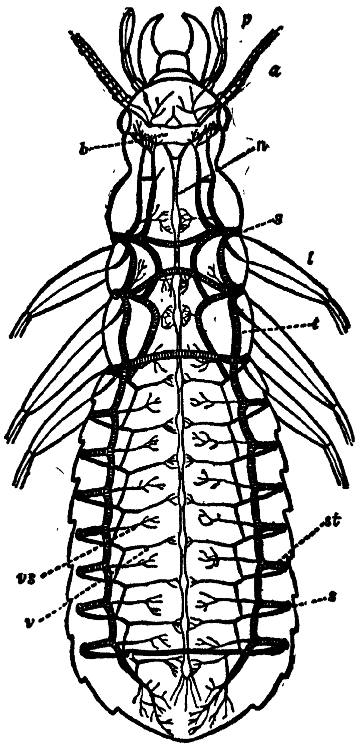

FIG. 76. *Tracheal system of an insect:* (*s*) *spiracles;* (*t*) *chief tracheal trunk;* (*v*) *and* (*vs*) *are branches of the tracheal trunk.* (*From Shull, Principles of Animal Biology.*)

Various Devices for External Respiration. Except for the insects and their allies, all metazoan adaptations to provide respiratory exchange for internal tissues involve the utilization of some type of circulatory system and the consequent development of external and internal respiration. The chief variations that occur among these organisms concern the type of respiratory devices that are utilized to accomplish external respiration.

1. *The Skin as an Organ for External Respiration.* In the earthworm and numerous other small metazoans, the body surface is thin and moist and has an area sufficient to provide for an adequate gaseous interchange between the blood and the external medium. Here no breathing is required, since the whole body surface is adapted for respiratory exchange. It is worth noting in this connection that the very properties that make the earthworm's body covering a good respiratory membrane make it impossible for the animal to exist in any except moist, protected situations.

2. *Gills as Organs for External Respiration.* Gills are special respiratory membranes adapted for a gaseous exchange between the blood[1] and an external aquatic medium. The gills of fishes are broad plates of delicate respiratory tissue richly supplied with blood vessels, attached in the region of the pharynx to bony arches; between these are slits through

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[1] In most aquatic insect larvae, the air of the tracheal system is brought into close proximity to the water in thin delicate outgrowths from the body wall, which are termed *tracheal gills*.

which water taken into the mouth is passed out. Many aquatic animals have gills which, though differing in position and complexity, function on the same general principle as do those of the fish. Examples are to be found among the worms, clams, certain aquatic insect larvae, and tadpoles.

3. *Lungs as Organs for External Respiration.* True lungs are found only in the air-breathing vertebrates. We have seen something of their structure and functioning in man, and, although the lungs of certain of the lower vertebrates are much simpler, they show a comparable structure and have the same function. Certain other land animals, such as the spiders and terrestrial snails, also have respiratory organs that function as lungs, although these differ markedly in origin and structure from the lungs of vertebrates.

Excretion

Besides excess water and carbon dioxide, there must be removed certain solids in solution, particularly nitrogenous wastes such as urea and uric acid. The methods found in various animals for the excretion of this type of waste are discussed below.

Excretion in the Protozoa. In the Protozoa, excretion doubtless occurs to a greater or less extent through the surface of the body, but usually one or more small *contractile vacuoles* concerned with this function are also present. Such a vacuole fills with a watery fluid drained from the surrounding protoplasm and periodically discharges it to the outside, thus washing the protoplasm free from soluble waste materials. In fresh-water Protozoa an equally important function of these cell organs is to "bail out" the water which continually enters the cell as a result of osmosis, and which otherwise would soon cause rupture and death of the organism.

Excretion in the Metazoa. In very simple multicellular animals, the surfaces of the body suffice for excretion; hence they have no special excretory organs. All except these simplest Metazoa, however, have developed certain systems and organs for the removal of wastes. Some of the more important types of these systems are as follows:

Protonephridial System. This type of excretory system is characteristic of the flatworms and does not require a circulatory system for its operation. The metabolic wastes are carried from the tissues to the outside by means of a system of tubes. This drainage system may be simple or greatly branched, but each tubule originates from a large, cup-shaped cell, the inner wall of which bears a tuft of long cilia. The beating of these cilia suggests the flickering of a flame; hence the cell is called a *flame cell.* Besides withdrawing fluid from the surrounding tissues, the vibrations of the flame-cell cilia create a current that carries the collected wastes to the outside.

Nephridia. In the metameric worms (for example, the earthworm) nearly every segment of the body is provided with a pair of coiled tubes, the nephridia, each of which has a funnel-shaped, ciliated opening, the *nephrostome*, which projects through the septum into the cavity of the segment ahead, and there opens directly into the body cavity or coelom. The other end of the coiled tube opens to the exterior through the body wall. The nephrostome sweeps in liquid and small particles by the action of its cilia, and cilia within the tube assist in propelling liquids to the exterior. Portions of the nephridium are composed of cells that take up water and certain dissolved materials from the fluid in the tube and return them to the blood, thus concentrating the wastes and conserving useful substances. The nephridia are richly supplied with blood vessels.

Kidneys. The excretory organs of the vertebrates are the kidneys, which operate in the manner already described for man.

Coordination and Irritability

We have seen that the various structures employed to accomplish digestion, respiration, and excretion show a wide range in complexity and efficiency. In even the simplest animals, it is essential that all these functions (and others) be coordinated to supply the needs of a complete organism. This need for coordination involves the animal's response to the environment; for the rates of digestion, respiration, etc., are largely determined by stimuli that originate in the environment and (because of the irritability of protoplasm) produce appropriate responses on the part of the animal. In the lower animals, the problem of coordination, although very complex, is *relatively* simple; but as digestion, and other processes come to involve more and more complicated structures, the magnitude of the problem of coordination increases proportionately. In general, the greater the degree of coordination the more varied the environment in which the animal can maintain itself.

Responsiveness in the Protozoa. The single-celled animals show a surprising degree of adjustment to external factors and have at times a rather complicated behavior. Temperature exerts a general effect on protoplasmic activities, controlling rate of reproduction, locomotion, and physiological processes. Chemical stimuli are important, though there are no special receptors. Mechanical stimuli affect the general irritability of the protoplasm or are received by cilia and flagella (locomotor organelles found in certain groups of the Protozoa). Protoplasm is often directly responsive to light. The stimuli received by the cell may be conducted from the stimulated point to other parts of the cell without the intervention of any specialized structure. However, in some of the more complex protozoa (Ciliata) a "neuromotor" apparatus is present, which consists of protoplasmic fibrils leading from ciliated regions to zones of specially contractile protoplasm. Characteristic movements are produced in response to all the stimuli mentioned above.

Nerve Net. In the lower Metazoa, special cells have been differentiated for the reception and conduction of stimuli. These sensory cells are located in the body wall, and in the inner layer of cells surrounding the coelenteron branches extend between the sensory cells and from them to the contractile processes of the body-wall cells. Thus a network of sensory cells and cell processes is formed between the two layers of the body. Because of the lack of concentration of sensory cells, the nerve net conducts diffusely; chemical, mechanical, and light stimuli affect it most strongly.

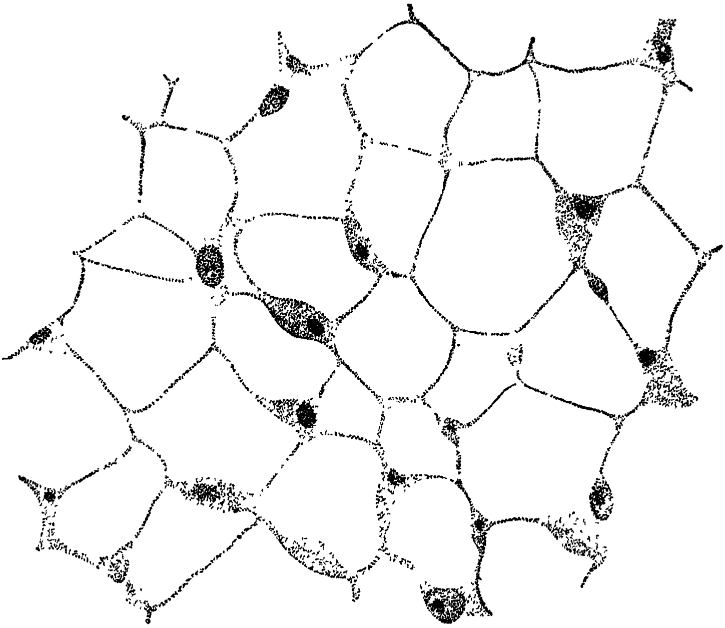

FIG. 77. *A portion of the nerve net of Hydra.* (*From Wolcott, Animal Biology.*)

Simple Nerve Cords and Cephalization. In the intermediate Metazoa, there first appears a concentration of nervous tissue and sense organs in the anterior end of the body—the formation of a *head* end (cephalization). This is first seen in the flatworms, elongated ribbonlike animals, in which the anterior end of the body is specialized. The head end of the flatworm is the part of the body most richly supplied with sense organs, and sensitivity decreases toward the posterior end. There is a massing of nerve cells at the anterior end to form a *cephalic ganglion*, which dominates the nerve system of the animal and which receives nerve impulses from the sensory organs of the head. The head end thus comes largely to control behavior, and impulses from the cephalic ganglion are transmitted through the two lateral nerve trunks to all other parts of the body.

The Ventral Nerve Cord and Its Cephalic Ganglion. In the segmented worms (for example, the earthworm) and the arthropods (for example, an insect), there has been a marked advance in the degree of cephalization of nerve tissue and sense organs, which reaches a maximum in certain insects and spiders. The enlarged and complicated cephalic nerve mass may be termed a *brain*. Leading from the brain, which is located above the esophagus or pharynx, two nerve strands encircle the digestive tube and unite below into a secondary ganglion. From this subesophageal ganglion, a double nerve cord runs down the ventral surface of the animal, swelling into small ganglia and giving off lateral nerves in each of the body segments; it is thus somewhat chainlike or ladderlike in appearance. As one proceeds from lower to higher groups within the insect series, there is a tendency for this system to become more and more highly concentrated in the anterior portions of the body; the ganglia and nerve cords at the same time become larger and more compact. Many of the insects with the largest and most concentrated nervous systems (for example, ants, wasps, bees) also show the most complex and highly adaptive behavior, even extending to social and psychic phenomena. These facts suggest that efficient control of a complicated organism requires a concentrated rather than a diffuse nervous system.

Concentrated Neuron System of the Vertebrates. Concentration of nervous tissue has gone much farther in the vertebrates than in any other group of animals. Within this group, we note an increasing degree of complexity in the structure and function of the nervous system, in general running parallel to complexity of body organization, and culminating in the very highly concentrated and strongly cephalized nervous system of man.

Summing up our survey of form and function in the animal kingdom, we see that no matter what animal we choose to examine, it proves to have the same essential needs and presents the same problems. Every individual animal has to obtain organic food (proteins, carbohydrates, and fats), to prepare this food for assimilation, to utilize part of it for maintaining its own protoplasm and part as fuel for the production of energy. Every animal requires oxygen for internal combustion and must eliminate the products of protein, fat and carbohydrate catabolism.

Every animal shows irritability and appropriate responsiveness to external and internal stimuli. And finally, every animal must have the ability to produce other animals like itself.

In no fundamental respect, therefore, do the other patterns of animal life differ from that typified by man so far as the basic problems of maintenance are concerned. The marked differences in the types of structural organization that are capable of carrying on the functions listed above are due almost wholly to different patterns and degrees of cell, tissue, and organ differentiation and the resulting degrees of "division of labor." Generally speaking, the higher the degree of such differentiation the greater the efficiency of the organism and the greater its freedom from narrow limitations as to where it can maintain itself in nature.

THE MAJOR PATTERNS OF PLANT LIFE

We have just seen that among animals the tasks of individual maintenance may be accomplished by a variety of types of organization, and the same is true of plants. However, all typical plants possess chlorophyll, and manufacture food by photosynthesis. This fact accounts not only for all the major features of their organization but also for the absence of many of the features characteristic of the animal. As we have previously pointed out, the plant has no need of nervous system, special sense organs, or locomotor organs, for it does not have to seek its food and is forced by its method of nutrition to remain fixed in one spot. It requires neither digestive system nor excretory system, for its food is made within its cells, and its wastes are for the most part either re-utilized, stored in tissues, or diffused into the atmosphere from the leaves. Its problems are, in fact, far simpler than those of the animal. This not only explains why even the highest plants are far less complex than the higher animals, but also enables us more easily to see that the same problems are common to all plants than was the case with animals.

Although typical plants all possess chlorophyll, there are a few that have lost the ability to produce this substance and that must, therefore, obtain their food in some other way than by photosynthesis. The distinction between the "green plants" and those that lack chlorophyll is functionally a very important one, and we shall use it as the basis for considering the major plant patterns under these two heads.

Types of Organization among the Green Plants

As we have already noted, the plant kingdom is divided into four major groups, or phyla, which are, in order of increasing complexity of organization, (1) the *thallophytes* (algae and fungi), (2) the *bryophytes* (liverworts and mosses), (3) the *pteridophytes* (ferns and fern allies), and (4) the *spermatophytes* (seed plants). In part, these phyla are distinguished by the type and degree of individual organization shown by their members, in part by differences in their life cycles and methods of reproduction. Their characteristics and subdivisions are discussed and illustrated in the Appendix.

In a broad sense we may compare the thallophytes with the Protozoa and the simplest Metazoa among animals, since this phylum contains the unicellular and the simplest multicellular plants. Some of these may be thought of as being on the protoplasmic level and others on the cellular level of construction. All the remaining plants have their cells arranged into definite tissues. The bryophytes are roughly analogous to the flatworms among animals—*i.e.*, they possess definite tissues, plus the beginnings of organs. Beyond this point it is not profitable to carry the comparison. It is true that the two highest groups of plants (the pteridophytes and spermatophytes) possess definite plant organs and even a suggestion of organ systems in some instances; but the plants function largely on the tissue level, and nowhere in the plant kingdom do we encounter anything so highly organized and functionally specialized as the organ system as it exists among the higher animals.

Unicellular Green Plants. Among the great numbers of minute organisms that inhabit the sea and bodies of fresh water, there are many whose bodies consist of a single cell. Some of these are clearly animal-like, in that they contain no chlorophyll and feed upon previously synthesized organic material, which they take into the cell for digestion; they are for the most part motile, and they lack cellulose cell walls. These are the Protozoa, or unicellular animals, which constitute the lowest phylum of the animal kingdom. Many of the other unicellular organisms are just as clearly plantlike, making their own food from carbon dioxide and water by means of chlorophyll, and possessing morphological features in common with the cells of higher plants, such as a cellulose cell wall. These organisms, sometimes called the *Protophyta,* are classified as algae, along with certain multicellular forms, and are placed in the lowest plant phylum, the Thallophyta. As in the Protozoa, these unicellular plants have, as single cells, to carry on all the functions necessary for life—to manufacture food, carry on respiration, excrete metabolic wastes, respond appropriately to the stimuli from the environment, and reproduce their kind. Again, as with the Protozoa, these unicellular plant cells must, in general, be more complex in structure than the cells of higher plants, in which there is cell specialization with corresponding division of labor.

For two reasons, the Protophyta do not constitute a clear-cut and easily definable group of organisms. On the one hand, they are closely tied in to the simple multicellular plants through numerous transitional types, starting with simple colonies of cells that are all alike and are almost indistinguishable from other cells that are free-living, and progressing through colonies showing incipient cell-differentiation and division of labor to the lowest multicullular algae. So numerous are the intermediate types and so close the evident relationships among many unicellular and simple multicellular forms that it is not possible to separate the Protophyta as a distinct plant phylum, as we do the Protozoa among animals.

On the other hand, the Protophyta are hard to differentiate sharply from the Protozoa, and this is the place, which we mentioned in introducing the study of plants, at which the distinction between plant and animal tends to become obscure. Some of the green unicellular organisms, except for the presence of chlorophyll, are almost indistinguishable from other organisms that lack chlorophyll and that must consequently be placed in the Protozoa. But this is not the cause of the greatest difficulty. There exist numerous transitional types, which combine plant and animal features in a single cell. This is true, for instance, of Euglena—a common fresh-water organism with a body composed of a long, flexible, spindle-shaped cell, to one end of which is attached a lashing flagellum that pulls the organism through the water. Near the end bearing the flagellum there are a reddish, light-sensitive eyespot, and a small, sometimes rudimentary "cell mouth" through which food particles can be taken in. Under ordinary circumstances, Euglena seldom feeds; its body is filled with chloroplasts containing an abundance of chlorophyll, by means of which it carries on photosynthesis.

It is evident, then, that among these lowest organisms, we can no longer distinguish clearly between animals and plants. Because of this difficulty, all the unicellular organisms are sometimes grouped under the name Protista, thus avoiding the dilemma by not attempting to differentiate between animal and plant. Since there are equally strong reasons for associating the Protophyta with the multicellular algae, it will usually be a matter of convenience as to which method of treatment is followed. The important thing is not what the organisms shall be called but the fact that at the base of the divergent animal and plant series the gap between these two types of life is at least partially bridged.

Simple Multicellular Green Plants. At the next higher level of organization above the single-celled and cell-colony types of plants, we find the *multicellular algae*, represented by the seaweeds, pond scums, and their like. These are aggregates of few or many more or less similar and semiindependent cells, forming a plant body of the type called a *thallus*, without roots, stems, or leaves and with little evidence of cell specialization and division of labor. The beginnings of the latter are found in some of the higher forms, such as the brown and red algae, in which certain cells form a rootlike *holdfast* for attaching the plant to some support, and the body is divided into a stemlike portion and leaflike blades. The resemblance of these structures to roots, stems, and leaves is, however, purely superficial; the holdfast and "stem" are merely supporting structures, and the "blades" are not comparable to the blades of leaves, since they consist of semiindependent cells, as in other algae.

In all the algae, maintenance is accomplished principally through the independent functioning of the individual cells. The ability of the algae to get along without a high degree of organization is the result of their mode of life. They do not need an epidermis specialized to resist evaporation, for they live in water or in very moist situations; strong mechanical tissues are not required because of the prevailingly small size of the body and the fact that the larger algae are all aquatic and are buoyed up by water; a transporting system would be superfluous, since each cell has access, immediately or at a few removes, to the surrounding water with its contained gases and minerals.

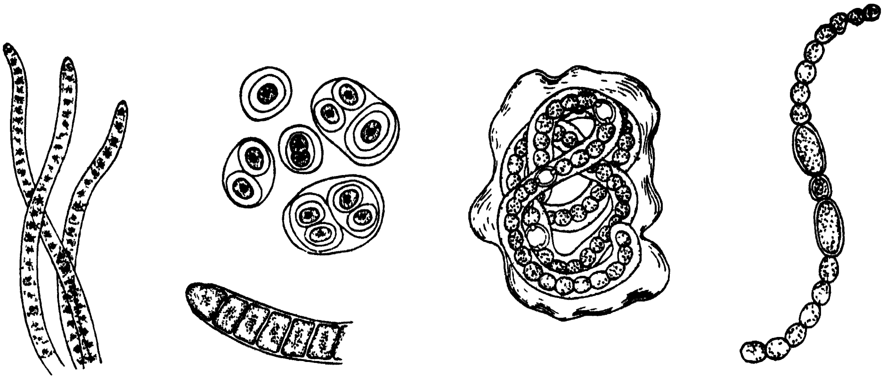

FIG. 78. *Some unicellular and simple multicellular plants (blue-green algae).*

Intermediate Multicellular Green Plants. The *liverworts* and *mosses* (bryophytes) are the simplest land plants. They are doubtless derived from some group of algae, but they differ from all the thallophytes in their higher degree of structural organization, related to the requirements of life upon land. The most important of these requirements is protection against excessive loss of water by evaporation. In most bryophytes, the body has become several cell layers thick, so that relatively less surface is exposed. The outermost layer has become specialized into an epidermis, composed of cells that secrete a thin layer of cutin, the cuticle—a structure also present in the higher plants, as we have seen.

The cuticle forms a relatively impervious coating over the exposed parts of the plant and prevents excessive water loss, but at the same time it hinders free interchange of oxygen and carbon dioxide between the plant tissues and the air. This difficulty is met by the development of stomata, of a very simple type but functioning as do those of the higher plants already described. The development of a cuticle and stomata, structures first found in the bryophytes and characteristic of all the higher plants, has made it possible for plants to live in air instead of water.

Another feature of the land environment that requires adaptation by the plant is the fact that only a part of the body is in contact with a medium (the soil) from which water and essential salts can be obtained. This makes necessary the development of special absorptive structures. No such structures are needed or found among the thallophytes, the rootlike holdfasts found in some of the algae playing no part in absorption. Here the bryophytes show another advance in organization; the parts of the plant that touch the soil develop numerous hairlike processes called *rhizoids*, which in part act as holdfasts but also absorb soil water. They are not true roots and compared with roots are relatively inefficient as absorbing organs.

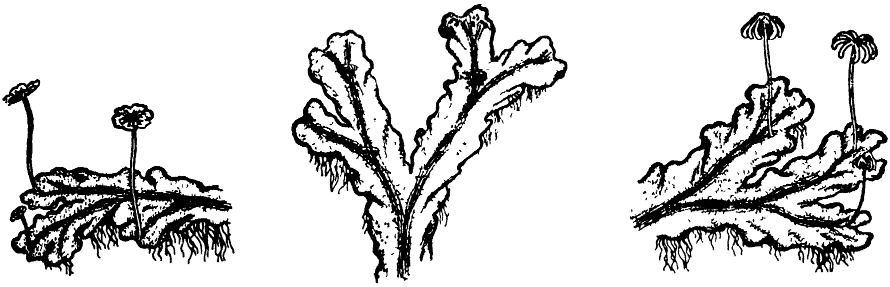

FIG. 79. *Some intermediate multicellular green plants* (*liverworts*).

Although the bryophytes are true land plants, they are in some respects quite imperfectly adapted to land life.[1] They are most numerous and successful in moist or wet environments; and although some of them live in situations that at times become very dry, they do so only by suspending all activity during the period of drought. At such times, they wither and apparently die, only to begin to function again with the return of adequate moisture. None of the bryophytes attains large size, and most are quite small. Among the factors responsible for this are the following: their mechanism for absorbing soil water is not very efficient and could not supply the needs of a large plant with extensive evaporating surface; they have no well-developed mechanical tissues to support increased weight; and, lastly, they have no vascular system to distribute water and food to the parts of a large body.

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[1] One important factor that prevents the bryophytes from colonizing the drier parts of the land is their dependence upon water for the accomplishment of fertilization, as will be explained in the section dealing with reproduction.

The Most Highly Organized Green Plants. At the highest level of individual organization, we find the members of the last two plant phyla, the pteridophytes (ferns and fern allies) and spermatophytes (seed plants). These two groups of plants are fully adapted to life upon land. In spite of a great amount of diversity in form and details of structure, they are, in general, built on the same basic pattern that we have already studied in detail in the case of the dicotyledons. The body is divided into root, stem, and leaf; it is covered with a protecting epidermis and cuticle or has other evaporation-resisting coverings that replace the cuticle; it contains mechanical tissues that support the body and permit the development of large size; and it contains a vascular system for transporting water and other substances from one part of

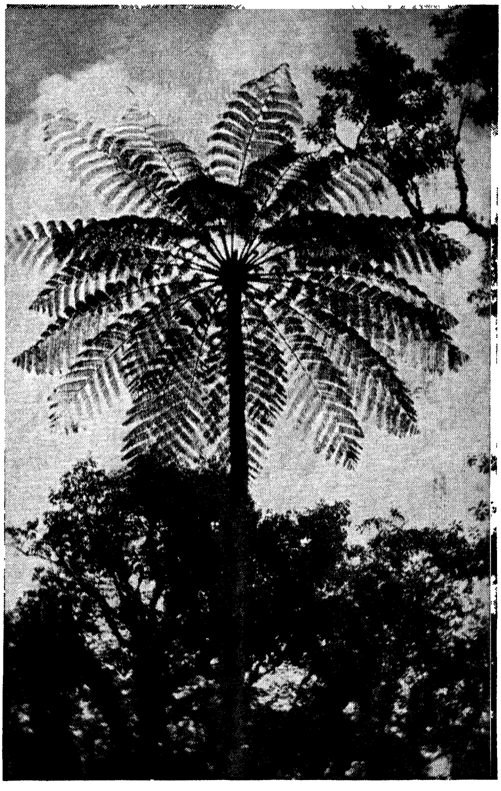

FIG. 80. *A tree fern (Alsophila) on Mt. Gedeh, Java. (Photograph by Dr. William Seifriz.)*

the plant to another. On account of the latter characteristic, which is shared by the pteridophytes and the spermatophytes, these two groups are often together called the *vascular plants.*

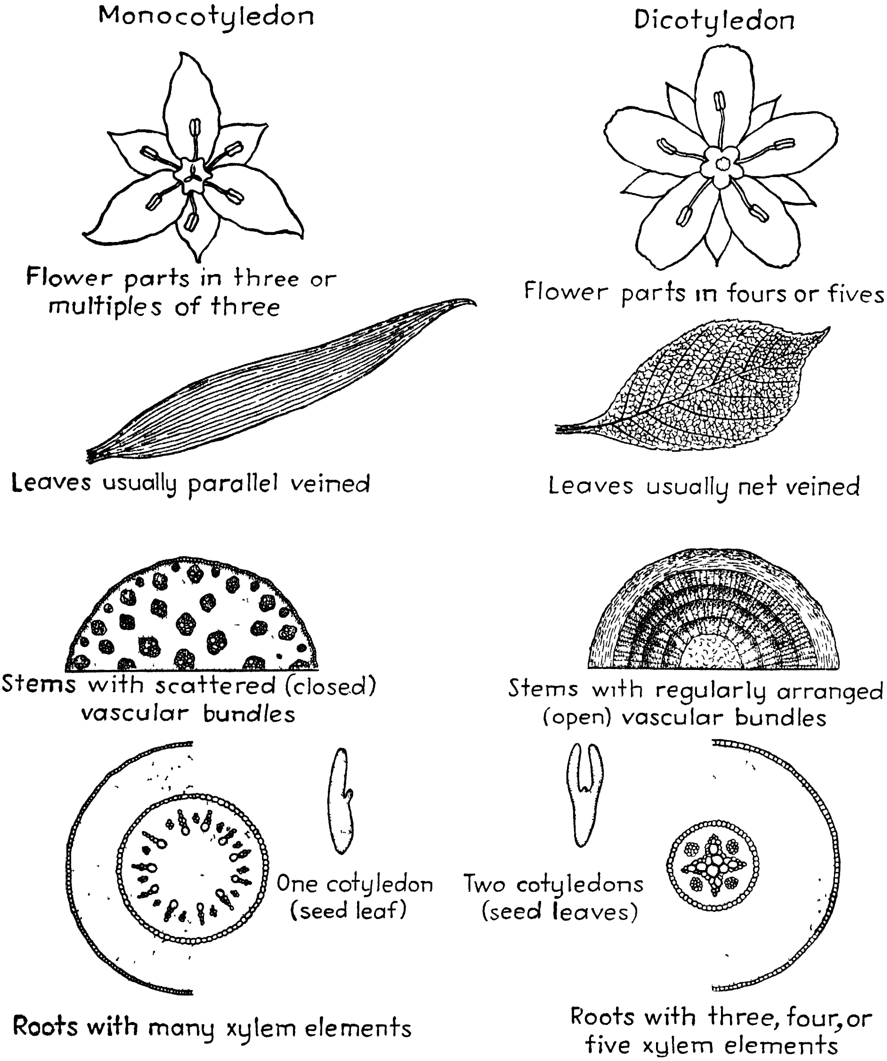
Monocotyledon
Dicotyledon
Flower parts in three or multiples of three
Flower parts in fours or fives
Leaves usually parallel veined
Leaves usually net veined
Stems with scattered (closed) vascular bundles
Stems with regularly arranged (open) vascular bundles
One cotyledon (seed leaf)
Two cotyledons (seed leaves)
Roots with many xylem elements
Roots with three, four, or five xylem elements

FIG. 81. *The monocotyledons and dicotyledons of the phylum Spermatophyta constitute the most complex members of the plant world. In this diagram they are compared. (Courtesy of the General Biological Supply Company.)*

The *pteridophytes* include the ferns, club mosses, horsetails, and a few other types of plants. Although, like the bryophytes, they are dependent upon the presence of water for reproduction, in all other respects they are far more advanced and are closer to the seed plants in type of individual organization. The roots of the fern have root hairs, an apical growing point and a root cap; there is a single central vascular bundle of radial type. In most ferns, the stem is a horizontal, subterranean *rhizome*,[1] which gives off leaves from its upper surface and roots from the underside. Beneath the epidermis of the stem, there is a cylinder of mechanical tissue; this encloses a mass of parenchyma cells and two or more vascular bundles at the center. Each of the latter is composed of xylem surrounded by phloem; there is no cambium layer, growth of the stem being accomplished entirely by the meristematic zone at its apex. True leaves are organs that appear for the first time in the peteridophytes. The leaves of ferns have a stalk and a more or less divided blade, the latter often of large size. Unlike those of seed plants, the fern leaf continues to grow for some time after it is formed; when it emerges from the ground, it is coiled like a watch spring, and it continues to elongate at the tip while its older parts broaden and unroll. Another peculiarity of the fern leaf is that each leaf vein, when it forks, divides into two approximately equal branches. The leaves of the fern, unlike those of flowering plants, bear reproductive bodies on their lower surfaces in the form of minute "fruit dots," or *sori*. There are no flowers in the pteridophytes.[2]

The *spermatophytes*, or seed plants, not only are the most highly organized of plants but also are the dominant plants of the modern world. Since we have already examined the structure and functioning of the members of this group in detail, it will be unnecessary to review these matters here.

Plants That Lack Chlorophyll

Although plants typically possess chlorophyll and manufacture food by photosynthesis, certain of them—clearly plants, as judged by structure and life history—lack this substance and must obtain their food in other ways. Such plants are encountered only among the members of the lowest and the highest of the plant phyla—the thallophytes and the spermatophytes. Physiologically, they fall into two groups—those which utilize some other source of energy than sunlight for synthesizing food from inorganic substances, and those which must obtain their food ready made in the form of organic compounds originally synthesized by green plants. The first group is a small one, comprising only a few very simply organized plants such as the iron and sulphur bacteria, which obtain the energy necessary for their metabolism by oxidizing inorganic substances and which are, in consequence, independent of sunlight. Most of the chlorophyll-less plants fall into the second group; they comprise a large division of the thallophytes (the fungi), and scattered examples among the seed plants.

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[1] In the tree ferns, the stem forms an erect trunk, attaining a height of 50 feet in a number of species and of 80 feet in the largest species known; the leaves of these tree ferns may attain a length of 20 feet.

[2] Although the pteridophytes are almost as well fitted for land life as are the seed plants, and in much the same ways, their peculiar mode of reproduction requires that the surfaces of the leaves be occasionally wet, and one of the stages in the life history is a delicate plant that can grow only in a moist environment. These requirements account for the fact that most pteridophytes live in relatively moist situations. The great advance of the seed plants over the pteridophytes lies in the perfection of a reproductive mechanism that can function in dry situations, and in the development of the seed.

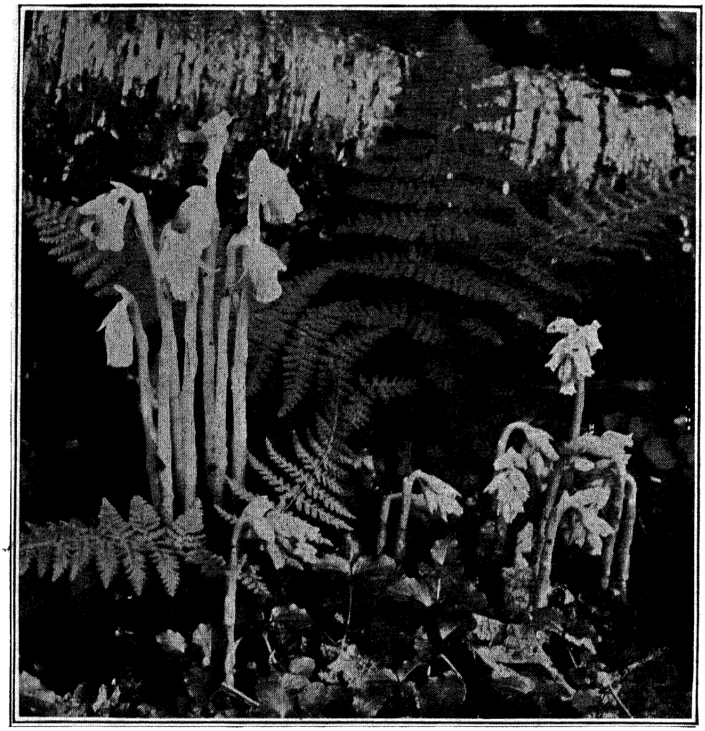

FIG. 82. *The Indian pipe, an example of one of the higher plants which lack chlorophyll and lead a saprophytic existence.* (*From Sinnott, Botany: Principles and Problems.*)

The *fungi* are defined as those thallophytes that lack chlorophyll. They are of many sorts; the best known are the bacteria, molds, rusts, yeasts, smuts, and those fungi whose spore-bearing organs form the familiar mushrooms, puffballs, and the like. The various groups of fungi are not all closely related; they probably originated at different times and from different kinds of algae, so that the group is not a "natural" one. Functionally, however, the fungi are sharply distinguished by the absence of chlorophyll and the modified nutritional methods that this lack entails. Some fungi are *saprophytes*, obtaining their food from the dead bodies of plants or animals or from plant and animal products. Bread mold and most of the mushrooms are examples of saprophytic fungi. Other fungi are *parasites*, obtaining their food from the living bodies of plants or animals. Among these are some bacteria and certain higher fungi that cause such plant diseases as wilts and rusts and such animal diseases as ringworm and athlete's foot. Although a large proportion of the fungi are saprophytic, there are thousands of parasitic forms, and few of the higher organisms do not at least occasionally serve as the hosts[1] to parasitic fungi. All gradations from strictly saprophytic to strictly parasitic existence may be encountered in the group. Being independent of photosynthesis, fungi as a group thrive in the dark.

No large group of the seed plants has lost the ability to produce chlorophyll, but here and there among the families of the flowering plants we encounter forms that have adopted a saprophytic or parasitic mode of existence and lost their green color. Saprophytes are relatively rare: well-known examples are the Indian pipe, which grows on decomposing plant materials in moist woods, and the Sierran snow plant. Beechdrops (parasitic on the roots of beech trees), broomrape (parasitic on clover roots), squawroot or cancerroot (parasitic on the roots of oaks and other trees), and dodder (a vine parasitic on herbs and shrubs) are examples of parasitic flowering plants that altogether lack chlorophyll. Such plants as mistletoe combine the parasitic habit with the ability to carry on photosynthesis, and illustrate the manner in which the transition to completely parasitic existence was accomplished.

Our survey of the chief patterns of plant life has shown that, excluding those plants that lack chlorophyll, all plants, from the simplest to the most complex, are faced with the same basic problems. As in the case of animals, they solve these problems in various ways, depending upon their degree of organizational complexity and the particular circumstances in which they live. We can go even further than this; in spite of the superficial dissimilarity between plants and animals, we are now in a position to realize that the fundamental requirements for living are the same for all organisms. Plant or animal, the organism must have access to water, it must obtain food, it must have means of releasing energy from that food (in the enormous majority of organisms, by means of oxidation), it must be able to rid itself of wastes, it must be able to respond appropriately to changes in its environment, and it must be able to reproduce. The types of organization characteristic of the plant and of the animal are merely the two extremes of the various methods that living things have devised for accomplishing these ends.

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[1] The organism that supplies sustenance to any parasite, animal or plant, is termed its *host*.

PART II

THE CONTINUITY OF THE RACE

Reproduction, Inheritance, and Variation

CHAPTER XVI

The Individual as a Member of a Race

We have thus far been primarily concerned with the processes that enable the organism to maintain itself as an individual. Much of any organism's structure and behavior are understandable, however, only when we examine its relationships to other individuals. One of the most essential of such relationships is that any individual organism is only a temporary unit in a sequence of generations. Each individual has a definitely limited period of existence. This may be as brief as several days or weeks for the individuals of some species, as much as "three score and ten" years or more for man, or even several centuries for a few kinds of long-lived trees; but in time the individual will cease to exist. The race to which the individual belongs, however, continues through countless generations, so that closely similar individuals successively appear, maintain themselves for a period, and then die—to be replaced by new individuals of the same kind. Here we encounter a new set of questions about organisms: How are these successive generations produced? Why and to what extent are the individuals of each new generation like those of the generation that preceded them? How is the organism's existence as an individual related to its membership in a race?

THE DISCARDED THEORY OF SPONTANEOUS GENERATION

Our modern concept of the origin and development of individual organisms is much more recent than our knowledge of their structure. At a time when a fairly accurate account of gross mammalian structure was being written (by Galen in 200 A.D.), nearly all educated men were still willing to believe that most or many forms of life arose spontaneously from nonliving matter. Frogs and insects were thought to come from mud, bees from the decaying bodies of oxen, such household vermin as mice and cockroaches from refuse. Even the wild geese (which breed in the then unknown arctic regions) were thought to be formed from a certain type of barnacle (still called the *goose barnacle*) that has a shape suggesting the head and neck of a goose. Ovid, who lived during the reign of the Roman emperor Augustus, expressed the accepted belief of his time when he wrote:

> By this sure experiment we know
> That living creatures from corruption grow:
> Hide in a hollow pit a slaughtered steer,
> Bees from his putrid bowels will appear,
> Who like their parent haunt the fields, and
> Bring their honey harvest home, and hope another spring.
> The warlike steed is multiplied, we find,
> To wasps and hornets of the warrior kind.
> Cut from a crab his crooked claws and hide
> The rest in earth, a scorpion thence will glide
> And shoot his sting; his tail in circles tossed
> Refers the limbs his backward father lost;
> And worms that stretch on leaves their filmy loom
> Crawl from their bags and butterflies become.
> The slime begets the frogs loquacious race;
> Short of their feet at first, in little space
> With arms and legs endued, long leaps they take,
> Raised on their hinder parts, and swim the lake,
> And waves repel; for nature gives their kind,
> To that intent, a length of legs behind.

Such beliefs appear again and again in the literature of the Middle Ages and seem to have been almost unquestioned until well into the seventeenth century. It was recognized, of course, that men and domestic animals were born from parents, but even here there were much mysticism and willingness to credit occasional instances to spontaneous origin. The first clear case of doubt of the actuality of the spontaneous origin of common small animals was that which led an Italian naturalist, Francesco Redi, to perform some simple experiments about 1680. (At this time, Vesalius' great treatise on human anatomy, based upon actual dissection, was already more than 100 years old.) Redi tested the spontaneous origin of maggots from decaying meat by placing bits of meat in three glasses. The first was left uncovered, the second was covered with fine netting, and the third was covered with parchment. He soon discovered maggots on the meat in the first glass, a few maggots on the fine netting over the second glass, and no maggots at all in the third glass, although in all the glasses the meat appeared equally spoiled. Further observations proved to him that the maggots originated not in the meat but from flesh flies which, attracted by the odor of the decaying meat, came to deposit eggs or living maggots; that the eggs hatched into maggots, the maggots fed and grew and transformed into flies, and that these flies, in turn, produced more eggs.

Although Redi's experiments marked the beginning of a growing disbelief in spontaneous generation, they by no means settled the question. About the time he was making his experiments, another naturalist (Leeuwenhoek) was beginning to make the powerful, simple lenses (Fig. 1) with which he was to discover the existence of the minute, subvisible, living organisms that we know today as the protozoa and bacteria. The first studies on these minute forms of life strongly suggested that they could arise by spontaneous generation, even though flies, worms, and frogs did not. It was found that one could always obtain such microscopic life simply by placing some clean, dry hay in a glass of clean, clear water. Soon after the water became more or less discolored by soluble substances from the hay, it would be found to be swarming with bacteria and later with protozoa, and even if the infusion were boiled, living organisms would appear a few days after it cooled. Such observations did much to offset the results of Redi's experiments on flies, for they at least seemed to support the possibility of spontanous generation in principle.

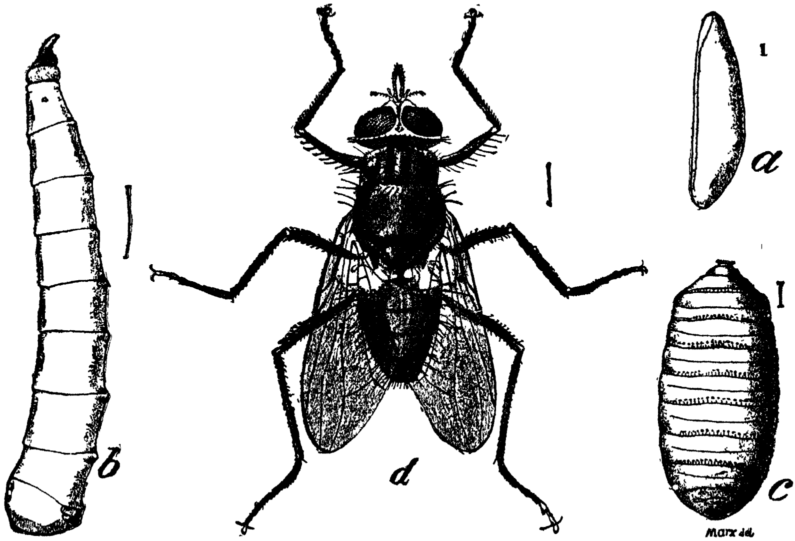

FIG. 83. *The life cycle of the horn fly.* (*a*) *egg;* (*b*) *larva* (*maggot*)*;* (*c*) *pupa;* (*d*) *adult.* (*From Riley and Johannsen, Medical Entomology.*)

Gradually, however, as compound microscopes became practical instruments and provided detailed images at high magnification, and as appropriate techniques were devised for the study of microscopic life, observations to test the spontaneous generation of even protozoa and bacteria became possible. About 1780, Spallanzani was able to isolate a single bacterium and watch it divide to form first two and then four "daughter" bacteria. He also made numerous experiments on sterilized (boiled) infusions that convinced him that even protozoa and bacteria could not arise spontaneously. Such experiments, however, call for a much more elaborate and precise technique than those that served Redi in his experiments with flies, and it was not until after the work of Pasteur, Cohn, Koch, and Tyndall,[1] in the latter half of the nineteenth century, that all biologists were convinced that *spontaneous generation was definitely disproved for all forms of living organisms.*

Today it is fully established that every living organism comes into existence through the reproductive functioning of parent organisms (or a single parent organism) quite like itself. It follows that each and every kind of organism that exists on the earth today is but a recent link in an unbroken sequence of once living, reproducing individuals. We do not know how life originally came into existence; but whether it was produced by a special creation by some supernatural power, or through spontaneous generation in some earlier and different stage of the earth's history, or whether the first living organisms were somehow transported to the earth from another planet, we are certain that under the conditions that now prevail "all life comes from life."

It is also clear that once the chain of continuing generations is broken, the race will cease to exist. Actually this has happened for many thousands of kinds of organisms in the past and will continue to happen to many races in the future.[2] The organisms that exist today are members of biologically successful races: some of the individuals of each generation of each race were able to maintain their own normal span of existence and to reproduce still another generation to carry on in turn.

In our study of the individual as a member of a race, it will be more profitable to look at organisms in general than to confine our attention to one or a few, as we did in the preceding section. We shall see that the reproductive processes of one organism will often help in the interpretation and understanding of similar but outwardly different processes of other forms. In the more than a million different kinds of individuals and races of organisms, with their great differences in size, complexity, and type of organization, we should expect to and do find great differences in the details of reproductive methods and adaptations. If we confine our attention to the common and essential processes, however, we find that all reproductive methods may be classified into a relatively small number of different types. These various types and processes of reproduction form the subject matter of the following two chapters.

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[1] The application of their work to surgery was first made in the eighteen sixties by Lister, in the introduction of "antiseptic surgery."

[2] Historical records and even living men bear witness to the recent existence of forms of life that have now ceased to exist. The passenger pigeon, the great auk, the dodo, and the zebralike quagga of South Africa have completely disappeared, and the Carolina paroquet, the ivory-billed woodpecker, and many other forms that are still, or possibly still, in existence appear to be doomed. It is when we turn to fossil records, however, that we see how frequent the extinction of races has been, and that probably far more kinds of organisms have perished without descendants than have survived to the present day.

CHAPTER XVII

The Reproduction of Animals

Although there are many essential similarities between the reproductive processes of the Protozoa and the Metazoa, the differences between a unicellular and a multicellular scheme of organization are nowhere more marked than in the different problems that they entail for the reproduction of new individuals.[1] As a consequence, it will be simpler and more accurate to consider the reproductive processes of the two groups separately, even though, if, following common usage, we employ the terms *sexual* and *asexual* in both Protozoa and Metazoa, it will be necessary to define them quite differently in the two groups.

REPRODUCTION IN THE PROTOZOA

Asexual Reproduction. Perhaps the simplest of all types of reproduction is the *fission* exhibited by many of the unicellular organisms. When an amoeba reaches its maximum size, it divides into two "daughter" amoebae of approximately equal size, and these, when grown to full

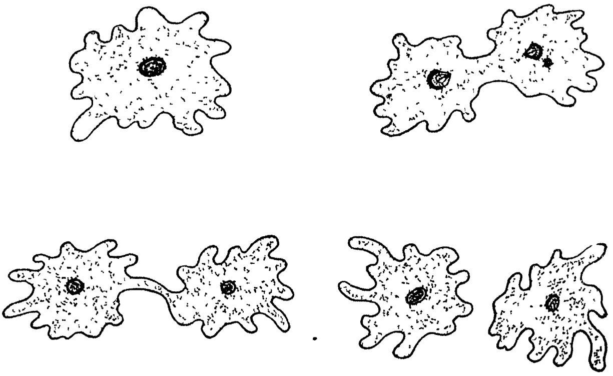

FIG. 84. *Binary fission in Amoeba.* (*Courtesy of the General Biological Supply Company.*)

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[1] The fundamental difference involved is discussed under Germ and Soma on p. 206.

size, will each, in turn, divide into daughter cells. In amoeba and most protozoa, this division appears to be essentially mitotic, the outwardly visible cytoplasmic division preceded by a more or less precise nuclear division. Fission is a typical method of reproduction in most protozoa, in the bacteria, and in many unicellular as well as filamentous algae.

Essentially similar to fission is the *multiple fission*, or *sporulation*, exhibited by various Protozoa and Protophyta. Here the parent cell, instead of dividing into two (binary fission), divides to form many minute masses of cytoplasm and nucleus, each capable of growing into a full-sized organism.

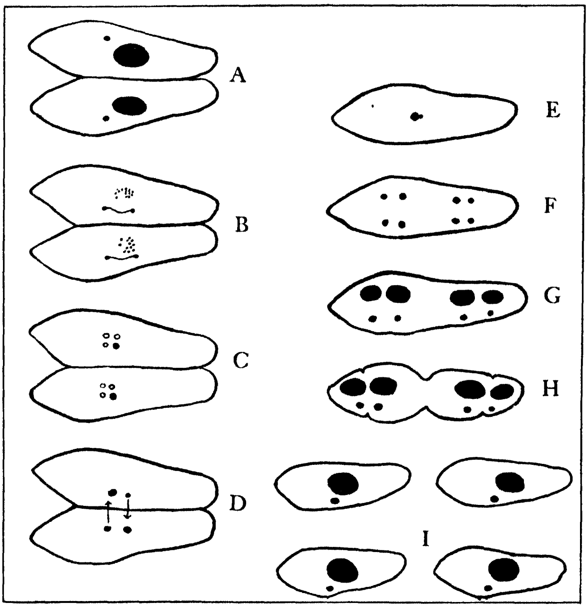

FIG. 85. *Conjugation and fission in Paramecium caudatum. Not all stages are shown. (A) Two animals unite by their oral grooves; (B) the large nuclei begin to degenerate, the small nuclei divide; (C) each small nucleus divides again and three of the daughter nuclei degenerate; (D) the remaining small nucleus in each animal divides again and one part migrates to the opposite paramecium; (E) the animals separate (only one is followed from here on) and the small nuclei fuse; (F) the product of the fusion of the small nuclei divides several times; (G) four of the resulting small nuclei develop into large nuclei; (H) the cytoplasm constricts twice; (I) four small paramecia, each with one large and one small nucleus, are produced. (Modified from Borradaile and others.)*

Fission, together with sporulation, is termed *asexual reproduction* in contradistinction to a form of fission that is preceded by either a temporary or a complete union of two individuals.

Sexual Reproduction. Another common type of reproduction in unicellular animals and plants consists of *conjugation and fission* (*i.e.*, fission preceded by conjugation). Conjugation consists of two individuals coming together either to (1) effect a mutual exchange of nuclear material; or (2) completely fuse into a single cell (two *gametes* fusing to form a *zygote*). In either case, the resulting cells (or cell) contain at least nuclear material from both conjugating individuals. Following conjugation, either binary or multiple fission of the conjugated cells (or cell) takes place. This differs from simple fission essentially in that the daughter cells contain material (at least nuclear material) from two different parent individuals.

Some unicellular organisms appear to reproduce chiefly or exclusively by fission; others reproduce chiefly by conjugation and fission; but many organisms utilize both methods, either alternately or as they are stimulated by varying environmental conditions.

"Potential Immortality" of Unicellular Organisms. Since reproduction is accomplished by division of the entire cell, the parent organism is replaced by two (or more) new "daughter" organisms. Full growth and maturity are followed by division rather than by senility and death. In this sense, a unicellular organism is potentially immortal. Actually, of course, the great majority of unicellular organisms are killed either by other organisms for food or by adverse conditions of their environment. Such death is a matter of chance rather than necessity.

REPRODUCTION IN THE METAZOA

Since the variety and complexity of reproductive methods exhibited by multicellular organisms is much greater than those found in the Protista, and since there are some rather fundamental differences in detail between the reproductive adaptions of the Metazoa and those of the multicellular plants, we have chosen to treat reproduction in animals and plants separately. It would be possible to classify metazoan reproduction into sexual and asexual on the same criterion that we used for the Protozoa, *i.e.*, on whether one or two parents are concerned. Although such a classification would be closer to our usage in everyday speech, a much more fundamental and useful basis for classifying reproduction in the Metazoa is found in the concept of germ and soma.

Germ and Soma. We have seen that one of the chief characters of the multicellular organisms is the differentiation of their cells and tissues into diverse types, each differentiation accompanied by a corresponding division of labor, until in the higher Metazoa there are hundreds of kinds of highly specialized cells, each fitted for some definite and limited function. The most fundamental specialization and division of labor is that between the cells that are reserved and later specialized for reproduction, and all the remaining cells of the body. The reproductive cells, or *germ cells*, have no contributing share in the functioning of the body; housed and nourished in the body, their sole function is the production of a succeeding generation. All the remaining cells have some necessary share in the maintenance and functioning of the body of the individual they compose; they are known collectively as the *soma.* This distinction between *soma* and *germ* is progressively more clear-cut and definite as we consider progressively more complex organisms, and it is of great importance in the consideration of reproduction, inheritance, and evolution.

In the discussion that follows, as well as in the section on genetics, we shall use the term *asexual reproduction* for reproduction from soma tissues and the term *sexual reproduction* for reproduction by germ cells (or a germ cell). This will deviate from our everyday usage of the word *sexual* only in the case of one relatively unimportant type of germ cell reproduction (parthenogenesis).

Asexual (Soma Cell) Reproduction in Metazoa

Among the lower, less highly individualized Metazoa, there is a relatively slight development of cell differentiation and division of labor. In such organisms, various methods of producing new individuals directly from the soma tissues of the parent individual are an important, often the most common, method of reproduction. Such asexual reproduction shows considerable variation in detail among the various groups of lower Metazoa, but practically all types may be classified as either *budding* or *fission.*

Budding is the formation of new "daughter" individuals by the growth and proliferation of some portion of the parent's body. The parent continues to exist as an individual. Budding is a common and extremely important method of reproduction and propagation in *all groups* of plants; in animals it is confined to the lowest, least individualized groups of the Metazoa, especially the sponges and coelenterates (Hydra, corals, and their kin). In the sponges, a peculiar type of "internal budding" is the chief method of reproduction.

Fission is the production of two new "daughter" individuals by the self-cutting in two of the parent individual. In this process, the parent individual ceases to exist and is replaced by the two *new* daughter individuals. Fission is not so widely utilized a method of asexual reproduction as is budding but is characteristic of the flatworms and a few other forms.

Limitations to Asexual Reproduction. Asexual reproduction in the Metazoa is limited to those forms that have relatively little complexity of body parts, in which the tissues are comparatively few and are generally distributed over the whole body. In such simple organisms, budding and fission are capable of providing a new individual with all the kinds of tissues and organs that are found in the parent. In the higher Metazoa, with their marked differentiation of soma tissues and highly integrated and interdependent organ systems, asexual reproduction does not occur.

Other limitations to asexual reproduction are as follows: (1) In many organisms, asexual reproduction is limited to seasons of continuously favorable environmental conditions and is stopped by seasons of unsuitable temperature, or insufficient food or oxygen, when the species must resort to the sexual production of zygotes or eggs to survive. (2) In several groups that utilize asexual reproduction, it always alternates with sexual, so that each asexually produced individual reproduces, in turn, by sexual methods, and vice versa. The alternation of sexual and asexual generations that occurs in most coelenterate animals is known as *metagenesis*. (3) Asexual reproduction does not produce so great a diversity and variation among the offspring as is produced by sexual, and especially by bisexual, reproduction.

There is considerable parallelism between asexual reproduction and the power of organisms to reproduce lost or mutilated parts. When a hydra or a sponge is cut into minute portions, each portion, if it contains cells of all kinds of essential tissues, is able to regenerate a complete new individual. Such an individual will be, of course, very small but will be able to grow to full adult size. A flatworm can be cut into a number of portions, each of which is capable of forming a new, complete individual, provided that it contains all the considerably larger variety of essential tissues. We could, if it were desirable, propagate such animals from cuttings as we do plants. When we turn to higher animals, we find that the power to reproduce new individuals from severed portions of another individual rapidly decreases and is soon lost as we encounter progressively greater complexity of structure. In the lower ranks of the complex Metazoa, there is, however, a marked ability to regenerate lost legs, tails, and other appendages. This ability, too, diminishes with still further increase in structural and physiological complexity (or perhaps, more accurately, with increasing individualization of the organism) until in the higher vertebrates it is limited to the ability to heal a wound, knit a broken bone, and regenerate certain tissues.

Sexual or Germ-cell Reproduction in the Metazoa

Unlike the soma cells that are concerned in asexual reproduction, germ cells do not show differentiation into any sort of functional body tissue. They are to be classed neither as epithelial, contractile, sustentative, nor conductive tissue. All organisms that are reproduced by sexual means begin their existence as a single cell, and most of the multiplying descendants of this cell gradually differentiate into the various kinds of cells that make up the tissues needed in the formation of the new individual. However, not all the cells descended from the original germ cell differentiate into functional body cells; a few show no differentiation and form (or continue to be) the germ cells of the new individual. In the higher Metazoa, at least, these germ cells soon migrate into the soma tissues that are to form the gonads (ovaries or testes) of the new individual.

Maturation of the Germ Cells. When the young individual approaches sexual maturity, some (at least) of his or her germ cells begin a special process, peculiar to the germ cells, known as *maturation* or *meiosis.* Although the maturation processes of the spermatozoa (male germ cells) and of the eggs or ova (female germ cells) are fundamentally similar, there are sufficient differences in detail to necessitate separate descriptions.

Maturation of the Spermatozoa (Spermatogenesis). The unmatured germ cells that have resided in the testis since its formation are known as the *spermatogonia.* These multiply by ordinary mitotic processes and are produced in enormous numbers. When a spermatogonium is ready to begin maturation, its chromatin forms into chromosomes, and the chromosomes arrange themselves in pairs. In this stage, the maturing germ cell is called a *primary spermatocyte.* After this pairing process, or *synapsis,* each of the paired chromosomes undergoes a longitudinal split, so that each chromosome pair comes to consist of four bodies (four half chromosomes), together termed a *tetrad.* Any primary spermatocyte will thus have half as many (*haploid number*) tetrads, or pairs of chromosomes, as the soma cells and spermatogonia have single chromosomes. For example, in man, with 48 chromosomes (*diploid number*) in each soma cell and spermatogonium, synapsis results in 24 pairs of chromosomes (and 24 tetrads). Now follow two divisions of the primary spermatocyte. Typically, the first division is a *reduction division.* In it, the paired chromosomes separate, and one member of each pair goes to each of the daughter cells (secondary spermatocytes) that are formed. In other words, each secondary spermatocyte receives a *dyad* (two half chromosomes) from each tetrad that existed in the primary spermatocyte. The second division is called an *equation division.* In it, one of the two half chromosomes from each dyad goes to one daughter cell (*spermatid*), and the other half chromosome from each dyad goes to the other daughter cell. The equation division is very like an ordinary mitosis and accomplishes the same result, the equal quantitative and qualitative division of each chromosome or dyad. The spermatid now undergoes a marked change in shape and develops without further division into a *spermatozoön* (sperm, sperm cell). Each primary spermatocyte thus produces four functional spermatozoa. In some organisms tetrad formation may not occur, but synapsis, reduction division, and equation division always take place. Because of the reduction division, the spermatozoön has half the number of chromosomes that are to be found in the soma or the primitive germ cells.

The Matured (Functional) Spermatozoön. At the completion of spermatogenesis, the spermatozoön is ready to leave the testis and is capable of fertilizing an egg. The matured sperm is very small, usually one-thousandth or less of the bulk of the matured egg. It consists essentially of a very compact nucleus that forms the enlarged head of the spermatozoön, and of just sufficient cytoplasm to form a more or less whiplike, propulsive tail. The spermatozoa of practically all animals are motile (by swimming) and are attracted toward substances that diffuse from the unfertile eggs of their own species.

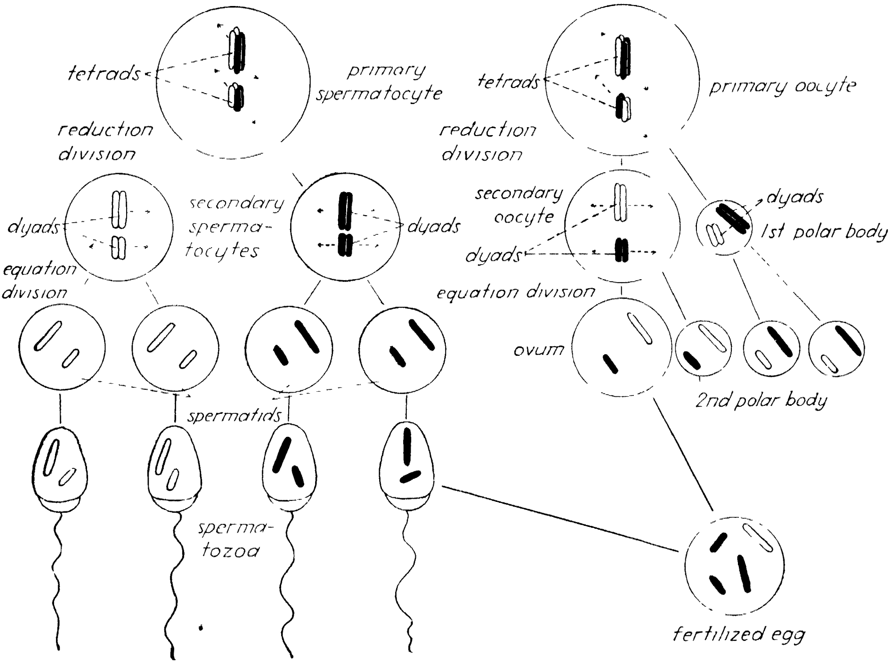
tetrads
primary spermatocyte
reduction division
tetrads
primary oocyte
reduction division
dyads
secondary spermatocytes
dyads
secondary oocyte
dyads
dyads
1st polar body
equation division
equation division
ovum
spermatids
2nd polar body
spermatozoa
fertilized egg

FIG. 86. *Diagram of maturation of the germ cells. Spermatogenesis is shown on the left, oögenesis on the right. The figure is designed to illustrate the behavior of the chromosomes, and the various parts of the diagram, especially the mature sperm and the polar bodies, are not drawn to scale.*

Maturation of the Egg (Oögenesis). The unmatured germ cells of the female gonad, the ovary, are known as *oögonia* and, like the spermatogonia, increase in number by ordinary mitotic division. After the oögonia have ceased to multiply by mitosis, some of them begin rapidly to increase in size by taking in and storing food material. These developing eggs are termed *primary oöcytes;* their nuclei soon begin synapsis and tetrad formation, precisely as in the case of the primary spermatocytes. Synapsis is followed by a nuclear division in which each tetrad is divided into two dyads; but one dyad from each tetrad remains in the egg, and the other goes to form a nucleus without cytoplasm that is extruded from the egg and becomes the *first polar body.* The female germ cell, after giving off the first polar body (thus losing one-half of each tetrad), is termed a *secondary oöcyte.* The nucleus of the secondary oöcyte immediately undergoes another division, and one-half of each dyad goes to each of the two daughter nuclei, one of which is extruded to form the *second polar body.* The now matured egg thus retains all the original cytoplasm and food material, and its nucleus consists of one-half chromosome from each of the original tetrads.

The first polar body usually divides to form two daugher nuclei, each with one half chromosome from each dyad, so that at the end of oögenesis there are four nuclei; three in the form of polar bodies without cytoplasm, one forming the egg nucleus. The polar bodies are later absorbed or degenerate, and only one functional egg is produced by each oöcyte.

It will be noted that the nuclear behavior is precisely alike in both oögenesis and spermatogenesis (although only one functional egg is produced in oögenesis) and that each egg and sperm nucleus contains one half chromosome for each pair of chromosomes that occurred in the unmatured germ cell.

The Matured (Functional) Egg. At the completion of oögenesis, the egg has been, or is ready to be, extruded from the ovary. It now consists of a reduced (haploid) nucleus, a comparatively large mass of cytoplasm, and (in most eggs) of a supply of stored food material in the form of oil droplets or yolk. The egg is thus many times larger than the spermatozoön and is invariably nonmotile. In several groups of animals, the egg is also provided (either before or after fertilization) with such accessory parts as a "white," a shell, etc.

Fertilization of the Egg. In the vast majority of animals, sexual reproduction is *bisexual, i.e.,* the matured egg is incapable of development until it has been fertilized by a spermatozoön. When spermatozoa are set free sufficiently close to such an unfertilized egg, they are attracted by it and swim in its direction. Only one spermatozoön is involved in the fertilization of any one egg; the first spermatozoön to reach it penetrates the egg membrane, and the head (nuclear portion) of the spermatozoön moves through the cytoplasm to meet the egg nucleus.[1] Soon after the two nuclei come into contact, they fuse to form a single diploid nucleus, which consists of one haploid set of chromosomes from the egg nucleus and another haploid set from the sperm nucleus. The diploid number of chromosomes that characterized the unmatured germ cells is thus restored. Fertilization is now complete, and the fertilized egg or zygote (Greek, *zygotos*, "yoked together") is ready to begin embryonic development.

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[1] Once within the egg membrane, the sperm nucleus absorbs fluid and swells to the size of the larger egg nucleus, so that it is soon difficult to distinguish between the two.

Dioecious versus Hermaphroditic Conditions. We ordinarily think of bisexual reproduction as being correlated with the existence of individuals of two sexes—male individuals that have testes and produce spermatozoa and female individuals that have ovaries and produce eggs. In the vast majority of bisexual animals, this dioecious (Greek, *di*, "two" and *oikos*, "house") condition is the rule, but there are species, genera, and even classes of animals in which the sexes are not separate but in which a single individual has both testes and ovaries and produces both spermatozoa and eggs. Such animals are spoken of as *hermaphroditic* and the condition, as *hermaphroditism*.[1] Among many of the snails, the annelid worms, the flatworms, and a few other groups, hermaphroditism is the normal condition.

Except for some of the flatworms, hermaphroditism rarely or never results in self-fertilization. The individuals of many hermaphroditic species do not mature sperm and eggs at the same time, but alternately; in other species, there are morphological or physiological barriers to self-fertilization, even though sperm and eggs are matured simultaneously, and mutual fertilization between two individuals is normally practiced.

Unisexual Reproduction or Parthenogenesis. Another comparatively uncommon type of sexual reproduction among multicellular animals is that which has been developed among several groups of insects and other invertebrates. This is unisexual reproduction, or *parthenogenesis*, in which part or all of the eggs of the species are able to develop without fertilization. Such eggs are clearly germ cells, for they have developed and matured in an ovary and are often outwardly and even microscopically indistinguishable from bisexual eggs, but unlike ordinary bisexual eggs, they undergo development without any stimulus from or union with a spermatozoön.

There is much evidence that parthenogenesis is a derived condition, developed in groups that were once bisexual but that have become able to dispense wholly or in part with fertilization. In some of these animals, males are unknown; in others, the males appear only in the fall to cooperate in the fertilization of bisexual eggs that will last over a winter resting period. In some species and groups (for example, certain gall wasps) there is an alternation between bisexual and unisexual generations; in others, as in the honeybee, fertilized eggs develop into females, unfertilized eggs into males (drones).

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[1] From the Greek myth of Hermaphroditus, son of Hermes and Aphrodite, who was united with the nymph Salmacis to form a single androgynous (male + female) person.

Artificial Parthenogenesis. Among a few animals—starfishes, sea urchins, and frogs, for example—in which the eggs will not normally develop without fertilization, it has been found that unfertilized eggs can be made to develop by certain special treatments. Such treatments include placing the eggs in various solutions for a certain length of time or, in the case of the frog egg, pricking the egg membrane with a needle that has been dipped in frog serum. Usually the individuals produced by such methods are feeble and often fail to complete their normal development,[1] but these experiments indicate that one of the roles performed by the spermatozoön is to stimulate development. Another role, that of contributing paternal, inherited qualities to the offspring, will be considered under genetics and evolution.

BREEDING HABITS IN THE METAZOA

We have seen that bisexual reproduction is by all odds the most common and important method of reproduction. It is the sole method available to the vertebrates and most of the higher and intermediate metazoans, and it is at least occasionally utilized by nearly all the lower metazoans that also reproduce asexually. There is good reason to believe that bisexual reproduction confers special advantages on the organisms that practice it. It permits the development of a much more complex degree of body organization than appears to be reproduceable by asexual means, and, by providing biparental inheritance, it has probably been an important factor in the evolution of the most successful types of animal life.

Whatever its advantages, it is also apparent that bisexual reproduction encounters a complication not presented by asexual or unisexual methods.[2] Fertilization of the egg requires the cooperation of two individuals, which not only must produce matured sperm and ova at the same season but must, by appropriate behaviors, bring the spermatozoa and eggs into close proximity. We find, therefore, that bisexual reproduction calls for special *breeding habits,* which lead the males and females of the species to abandon for a time their ordinary self-maintenance activities in order to perform their roles as parents of the next generation. Here we often find a clear subordination of the interests of the individual to the interests of the race. Many of the habits that have been developed to accomplish reproduction are highly dangerous or even fatal to the individuals that perform them and result in a heavy mortality of parent organisms.

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[1] Adult frogs, however, have been obtained by artificial parthenogenesis.

[2] Except in the rare, and relatively unimportant, instances of self-fertilization in hermaphroditic animals.

Although the breeding habits of many species of higher metazoans include parental care for the fertilized eggs and developing young, all bisexual breeding habits begin with the special activities that lead to the fertilization of the eggs.

Methods of Ensuring Fertilization. With more than a half million bisexual species, variously adapted to live in so many diverse types of situations, we cannot hope to survey all the interesting behaviors that have been developed to ensure fertilization of the eggs. We can, however, classify practically all known *types* of habits into four groups that, although they somewhat overlap, illustrate something of the variety and the range in complexity and efficiency of these methods. The most fundamental distinction is that between external and internal fertilization.

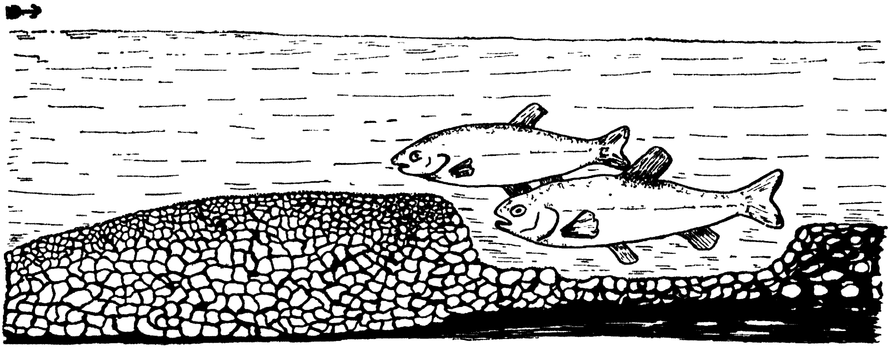

FIG. 87. *The breeding of the horned dace, Semotilus, an example of external fertilization with a modified form of amplexus. The paired fish are shown above a pit dug in a riffle by the male. The eggs are fertilized as they sink to the floor of this pit, and are later covered with pebbles by the male.* (*After Jacob Reighard.*)

External fertilization without amplexus is correlated with an aquatic (usually marine) habitat, a more or less sedentary type of life, and is usually associated with the congregating of large numbers of male and female individuals into a comparatively small area during the breeding season. There the females pour out their eggs into the sea water, and the males liberate tremendous numbers of sperms. The eggs drift about and diffuse out some substance that serves as an attraction to the spermatozoa of their own species. Sperms that chance to swim close enough to the egg to encounter this substance are attracted and guided to the egg and fertilize it. The approach of the sperm close enough to the egg to be attracted to it is a matter of chance, but chance that is very much increased by the proximity of the males and females and by the tremendous number of eggs and sperms that are produced.

External fertilization with amplexus[1] shows a much more elaborate and efficient development of breeding habits. Here, too, an aquatic situation is required, but, in addition, the male now actively seeks the female and clasps her or remains in very close proximity while eggs and sperm are discharged into the same very limited area, so that the eggs emerge from the female into a swarm of spermatozoa. A wide variation in details of this method is shown by the frogs, toads, and most of our fresh-water fishes.

Internal Fertilization without Copulation. Internal fertilization involves the liberation of the spermatozoa within the reproductive tract of the female. Here the sperms find a fluid medium in which to swim, and their path is so limited and directed that they are almost certain to encounter any eggs that are present. In a few forms, particularly some of the tailed amphibians, internal fertilization is accomplished by the males depositing sperm-filled capsules that the females find and take into their reproductive tracts. In some forms, this is done without the males and females coming into direct contact with one another; in others, the sperm-filled capsule (*spermatophore*) is transferred from male to female during a behavior that involves amplexus but not copulation.

Internal Fertilization with Copulation. In nearly all other forms, internal fertilization is accomplished by *copulation*, *i.e.*, by the direct transference of spermatozoa into the reproductive tract of the female by some intromittent organ (the penis, in the case of mammals) that forms a part of the male's accessory sex apparatus. In nearly all such forms, the actual copulation constitutes but a small part of the complicated courtship and reproductive behavior that culminates in fertilization.

Care of the Fertilized Eggs and Young. In many animals, the peculiar adaptive breeding behavior is continued into nesting habits and various types of care for the young. Once the egg is fertilized, development begins. The materials and energy required for at least the early stages of development either are supplied by food contained in the egg (stored there before the egg left the mother's body) or are furnished by the mother as development proceeds. In the former case, the egg is usually "laid," and we speak of such a habit as *oviparous*. Birds, amphibians, and most reptiles, fish, insects, and lower animals furnish examples of an oviparous habit. Among oviparous animals, the amount of food that is stored in the egg varies widely. At one extreme, we have

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[1] Literally, *amplexus* means "embrace" and is more correctly applied to the clasping of the female frog or toad in the arms of the male; however, its extension to include the behavior of many fishes during fertilization is physiologically if not morphologically justified.

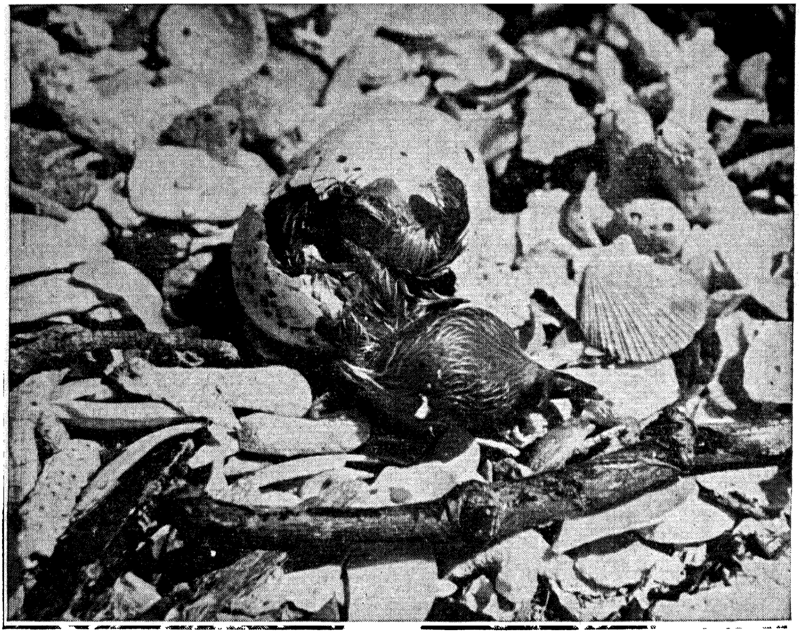

FIG. 88. *The egg of the sooty tern hatching on the beach at Dry Tortugas, Fla. The "nest" is composed of an accumulation of beach shells, corals, etc. The markings on the egg render it inconspicuous in these surroundings. (Photograph by J. C. Dickinson, Jr.)*

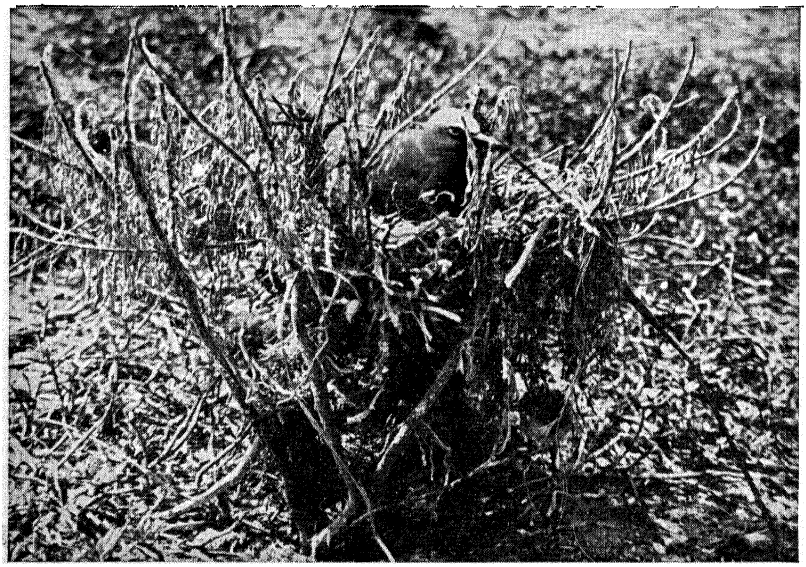

FIG. 89. *Nest of noddy tern at Dry Tortugas, Fla. (Photograph by J. C. Dickinson, Jr.)*

such eggs as those of the starfish, which contain very little food material (yolk). Such eggs contain too little food to carry development very far, and the young are hatched in a very primitive (larval) condition that is quite unlike the parent form. Other oviparous eggs contain much food material, stored in one part of the egg. Frogs, fish, birds, and reptiles, as well as the arthropods and most of the molluscs, produce eggs of this kind. In the frog's egg, the yolk forms little more than half the bulk of the egg; in the fish's egg, the yolk forms a much larger proportion; and in the eggs of birds and reptiles, the yolk forms all the true egg except a very small polar cap of cytoplasm, and the egg is supplied with additional food material, the "white," which is not truly a part of the egg but a secretion formed by the oviduct. In the frog, the egg hatches into a larval form, a tadpole, while the better supplied fish, reptile, and bird eggs hatch into baby animals quite like the parents in all but size and minor features.

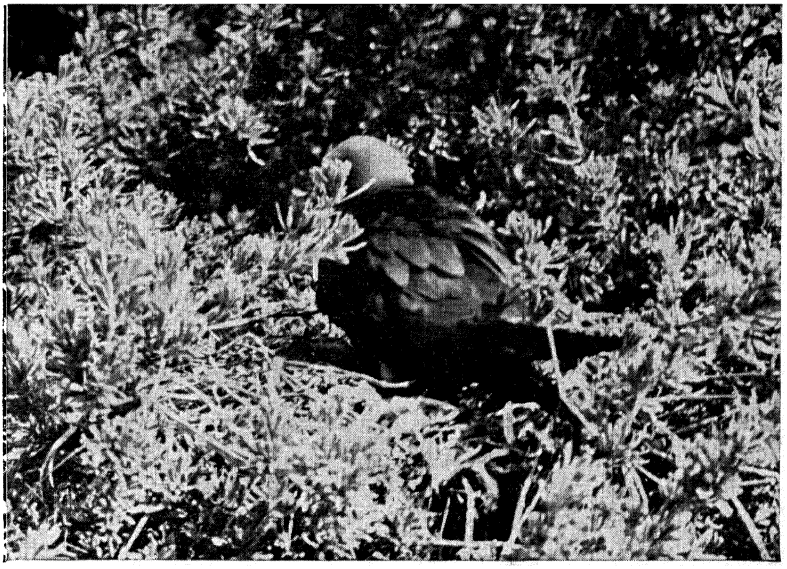

FIG. 90. *Nest of noddy tern at Dry Tortugas, Fla. Compare with Fig. 89. (Photograph by J. C. Dickinson, Jr.)*

In the case of mammals and a few other animals, the egg is not laid but is retained in the body of the mother, where it develops and from which it is "born" with the embryonic stages already completed. This habit is termed *viviparous*. The mammal egg contains very little yolk, just enough to carry it through the first few stages of development. The early embryo very quickly develops a circulatory system and a large area of extraembryonic membrane, the *placenta*, which grows into very intimate contact with the mother's uterine wall. Through the placenta, the embryo receives its needed supplies and rids itself of the by-products of metabolism.

A few organisms show a reproductive habit that appears somewhat intermediate between an oviparous and a viviparous habit. In some of the snakes, including the rattlesnake and its kin, and in some of the insects, an oviparous type of egg is formed that instead of being laid, is retained in the mother's reproductive tract until it hatches, although the embryo is "insulated" from any functional contact with the mother's tissues by the eggshell. This is essentially an oviparous habit but has outwardly the appearance of a viviparous one. This type of reproduction is termed *ovoviviparous*. In some of the sharks, another type of ovoviviparous habit is shown that is more nearly like true viviparity. In this case, the egg has a fairly large yolk but no white or shell, and, when the yolk has all been utilized, the embryo develops a belated placental connection with the mother's tissues.

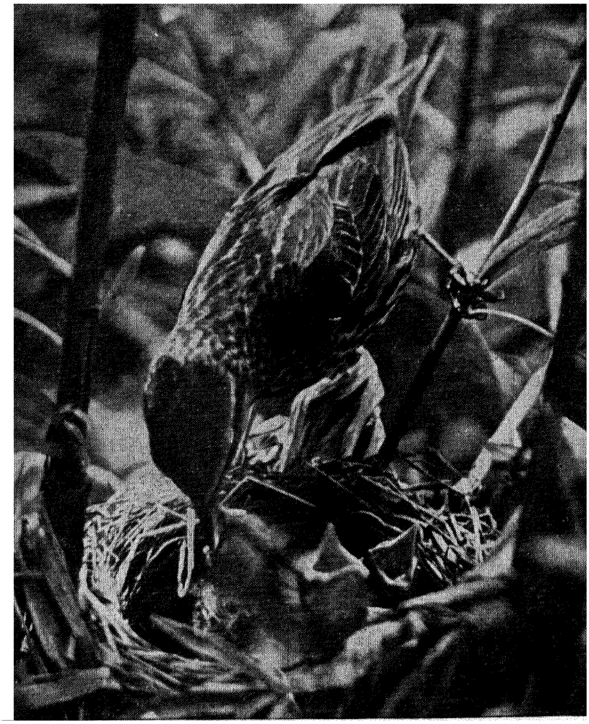

FIG. 91. *Parental care. The eastern red-winged blackbird feeding its helpless young. (Photograph by J. C. Dickinson, Jr.)*

Even when embryonic development is complete and the young are born or hatched, they still have to undergo a more or less prolonged period of postembryonic development before they reach the adult condition. In nearly all animals, this is a period of high mortality, and a large proportion, often a great majority, of the young perish. In general, animals have adopted one or both of two methods of offsetting this loss—a very high reproductive rate or some type of parental care of the young, at least while they are in the most helpless part of this period.

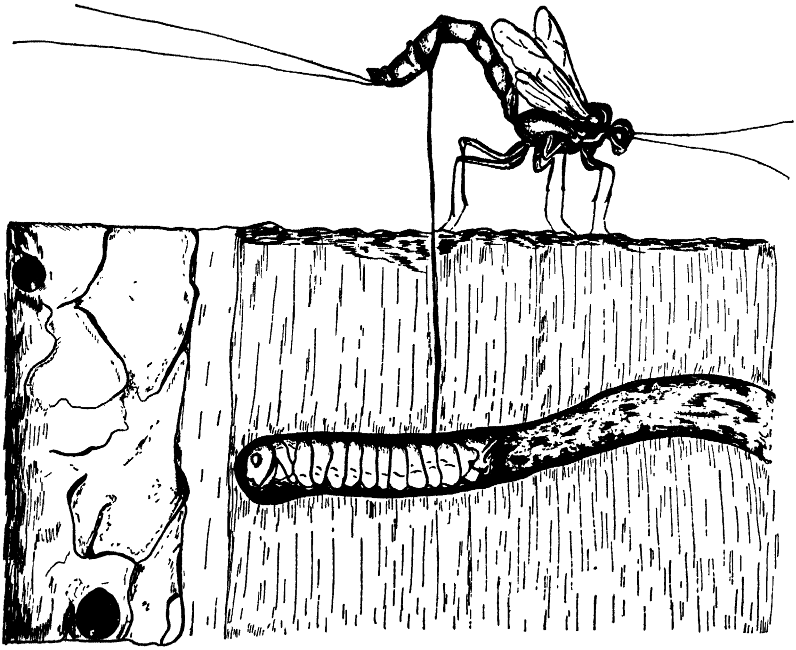

FIG. 92. *The female of an ichneumon-fly* (*Rhyssa*) *boring with its ovipositor in a fallen log and laying its eggs in the grub* (*larva*) *of the giant saw fly* (*Sirex*), *which has its burrow deep within the wood. When the eggs of the ichneumon fly hatch the young ichneumon larvae will feed upon the tissues of the saw fly larva.* (*Redrawn from J. Arthur Thomson, Outline of Science, G. P. Putnam's Sons.*)

In the higher vertebrates and in most of the fishes, where the egg is either well supplied with food (strongly telolecithal) or viviparity occurs, the young are hatched or born in a highly developed condition and with a clear resemblance to the adult. Even among these forms, however, there is great variation as to the degree of precociousness or helplessness that may be shown. For example, one has only to compare the newly born kitten, pup, or mouse or the newly hatched songbird, with equally young calves, colts, fawns, quail, chickens, or ducks.

In the amphibians and in most of the nonvertebrates, the young at hatching do not at all resemble the parent forms that reproduced them. Instead, they appear as larval forms (*larva, larvae*) that must pass through long periods of finding their own food before they are able to transform (*metamorphose*) into the adult form. In many of the lower invertebrates, the larval stage appears to be clearly correlated with the small amount of food contained in the egg, a condition that forces the young to become self-supporting at a very early stage; but in the insects and many other groups, the larval stage is associated with a highly successful type of

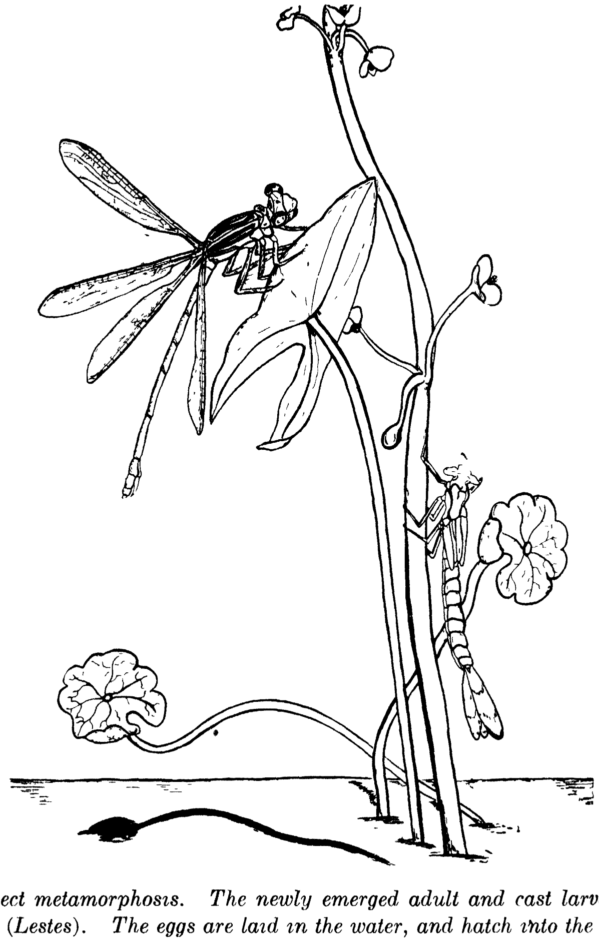

FIG. 93. *Insect metamorphosis. The newly emerged adult and cast larval skin of the dragonfly (Lestes). The eggs are laid in the water, and hatch into the aquatic larva. After living under water for some months (breathing by means of the tracheal gills visible at the tip of the abdomen of the larva), the larva climbs above water level on an emergent stem, its integument splits along the dorsal line, and the adult emerges.*

life cycle in which the larval forms are as highly organized for certain activities as the adult organisms are for others.

EMBRYONIC DEVELOPMENT

In the preceding paragraphs, we digressed from a consideration of the germ cells to look at some of the relationships and appropriate parental behaviors that result in the fertilization of the egg and the care of the developing young. We shall now return to the fertilized egg or *zygote* and see something of its subsequent development.

The period between the fertilization of the egg and the birth or hatching of the young is a time of rapid growth and change. During this period, in which the developing offspring is known as an *embryo* (Greek, *en*, "in" and *bruo*, "bud"), it changes from a one-celled zygote into a complex, many-celled organism more or less like the parent. It will be impossible for us to follow this development in detail for even one kind of organism, but we can see something of embryonic processes in general and learn to recognize embryonic stages that are common to all the metazoa.

Every zygote contains a *diploid nucleus*, a small mass of *cytoplasm*, and more or less *stored food material* in the form of yolk. The nucleus, as we have seen, was formed by the fusion of the haploid egg and sperm nuclei, but the cytoplasm and yolk were contributed solely by the egg, in which the proportions of cytoplasm and yolk and the details of their arrangement had been determined before fertilization. The proportions and organization of the cytoplasm and yolk are characteristic of the general group to which the animal belongs and will have two important consequences in the development of the zygote. Since in all oviparous eggs, the yolk provides the chief or sole material and energy for growth, the amount of yolk will determine how far the purely embryonic development can go before the young individual will be thrown upon its own resources or before the parents will need to provide another food supply.[1] On the other hand, since the yolk is nonliving and inert, it cannot take any active part in development, and, if present in a considerable amount, it modifies or, so to speak, distorts the processes that are carried on by the living cytoplasm.

There is good reason to believe that the homolecithal egg, described below, shows the most primitive organization of cytoplasm and yolk.

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[1] Parental care in the birds, certain of the insects, and a few other forms that have already provided a large store of food within the egg still further postpones the necessity of the young being "on their own" at the completion of embryonic development. The young of many of the Metazoa, however, must begin their independent existence long before development has reached anything like the adult structure of the parents.

The other types of eggs are apparently modifications of this original organization caused by the inclusion of large stores of yolk, which, although they variously distort its early stages, provide for a more adequate embryonic development. On this hypothesis, it is possible to correlate the many fundamental similarities that are common to the early embryonic development of all metazoans (except the sponges) and to interpret the relatively minor differences between them.

It should be noted that all eggs, and hence the zygotes derived from them, show *polarity*, *i.e.*, they are so organized that a certain point on the surface, the *animal pole*[1] is destined to be the center of the early externally visible embryonic activity. The opposite *vegetative pole* marks the center of the region of greatest concentration of yolk and hence of least early activity.

Homolecithal eggs contain a very small amount of yolk, and this is evenly distributed throughout the cytoplasm. Such eggs are very small[2] and undergo a markedly regular and symmetrical type of embryonic development that ends with the production of a postembryonic larval stage. This free-living larva must pass through a further period of development before attaining the structure of the adult. The eggs of starfishes, sea urchins, and marine worms are of this type.

Telolecithal eggs contain an abundant store of yolk that is massed toward one pole of the egg. The greater part of the cytoplasm is concentrated near the opposite ("animal") pole, with the nucleus near its center. Telolecithal eggs vary widely in the amount of yolk they contain. The frog's egg, which is mildly telolecithal, has little more than half of its bulk composed of yolk; the hen's egg (the "yolk" of the hen's egg is the true "egg") is strongly telolecithal, with the yolk comprising much more than 95 per cent of the whole egg and the cytoplasm occupying a small superficial disk at the animal pole. Fish eggs are somewhat intermediate, although not much less strongly telolecithal than the hen's or reptile's egg.

Centrolecithal eggs are characterized by having a comparatively large central core of yolk surrounded by a peripheral layer of cytoplasm. The development of the centrolecithal egg is even more strongly modified by its yolk than is that of the telolecithal egg. Insects produce eggs of this type.

Alecithal Eggs. The eggs of all viviparous mammals contain little if any yolk and superficially resemble homolecithal eggs. Their development, however, is much more nearly—though not entirely—like that of a strongly telolecithal egg, and this is undoubtedly related to the fact that the mammals are descended from oviparous ancestors that laid telolecithal eggs.

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[1] The egg nucleus is nearer this point than to any other part of the surface, and the extruded "polar bodies" are usually found here.

[2] Eggs of this type are usually correlated with a breeding habit that necessitates the production of huge numbers of eggs.

Early Stages and Processes of Development

Except for such modifications and distortions as are evidently due to the varied amount and distribution of yolk, the early embryonic stages of all metazoans (except sponges) are clearly similar. The brief account that follows is somewhat generalized but is based primarily upon the development of the homolecithal eggs of the starfish and of Amphioxus; the latter is a primitive relative of the vertebrates and shows the early development of certain characteristic vertebrate structures. The drawings of the development of Amphioxus (Fig. 94) and of the telolecithal egg of the frog (Fig. 95) should be studied and compared.

Cleavage. Soon after fertilization has taken place, the zygote divides by mitosis to form a 2-cell embryo. The plane of the first division, or first *cleavage*, passes through both poles of the zygote and divides it into approximately equal cells. The next cleavage also passes through both poles of the embryo, at right angles to the first cleavage plane, and divides each of the 2 cells to form a 4-cell stage. In the next division, each of the 4 cells divides in a plane at right angles to the first and second cleavage planes, and this results in an 8-cell stage. At the fourth cleavage, each cell is divided into two by planes that pass through both poles of the embryo, to produce a 16-cell stage. The fifth cleavage results in a 32-cell stage; the sixth, in a 64-cell stage, etc., but later cleavages are not likely to be so regular as the first four or five.

The Blastula. The rapidly multiplying cells of the embryo show a marked tendency to round off their acute inner angles so that a cavity is formed at the center of the spherical mass of cells. As cleavage follows cleavage, this cavity increases in size until, by the end of the cleavage period, when the embryo consists of several hundred cells, it has the form of a hollow ball. At this stage, the embryo is known as a *blastula* and its central cavity, which is filled with fluid, as the *blastocoele*.

Gastrulation. The completed blastula consists of a single layer of cells surrounding the blastocoele; but almost as soon as it is formed, it begins to change into a two-layered structure known as a *gastrula*. This change is accomplished by a flattening and then an indenting (invagination) of one pole of the blastula, until the blastocoele is obliterated and the cells of the indented side of the blastula wall are in contact with those of the opposite side. This indenting process, or invagination, is accompanied by a rapid multiplication of cells, so that the double-walled gastrula has approximately the same outward shape and size as the blastula from which it developed.

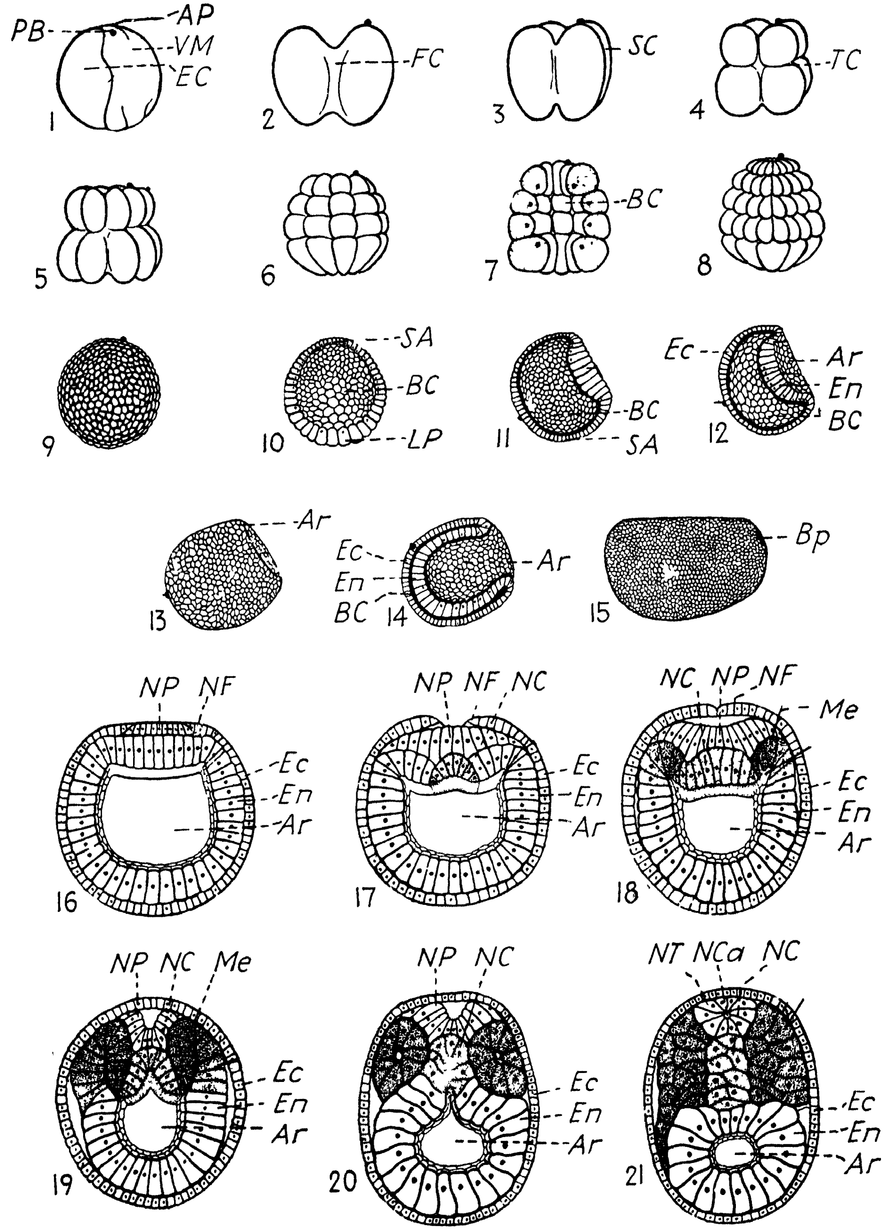
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FIG. 94. *Early embryology of Amphioxus. The development of the zygote as far as the gastrula stage. The first seven figures represent cleavage to the 32-cell stage; the next three represent the blastula; the last two the gastrula. (Courtesy of the General Biological Supply Company.)*

The outside wall of the gastrula is known as the *ectoderm;* the inner wall, as the *entoderm;* the latter lines a new cavity, the *archenteron,* which opens to the outside of the embryo through an opening, the *blastopore.*

Modification of Cleavage and Gastrulation. In telolecithal eggs, the processes of cleavage and gastrulation, although clearly comparable to those of the homolecithal egg, are modified by the large quantities of inert yolk. In the frog's egg, the early cleavage stages are not markedly different from those described above, but the later cleavages are unequal and result in a blastula with many small cells at the animal pole and few and larger cells at the opposite pole. The blastula wall is much thicker in the region of these large yolk-filled cells, and the blastocoele is thus displaced toward the animal pole. In more strongly telolecithal eggs, cleavage is confined to the small cytoplasmic disk at the animal pole, and the blastocoele forms a small shallow cavity beneath this disk. Gastrulation is correspondingly modified, considerably in the case of the frog embryo and greatly in embryos that develop from strongly telolecithal eggs. Nevertheless, a true gastrula is always formed with a distinct differentiation of outer ectoderm and inner entoderm and the formation of an archenteron and blastopore.

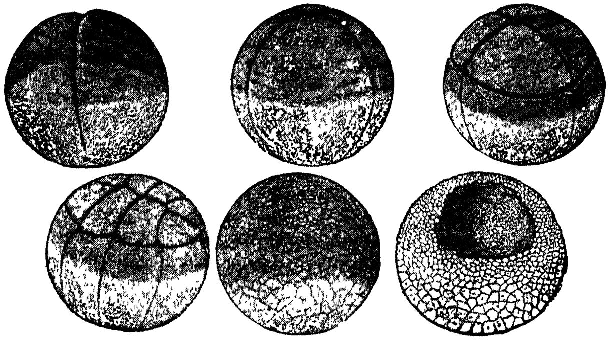

FIG. 95. *Early embryology of the frog. The development of the zygote through gastrulation. The amount of yolk present at the vegetative pole of the zygote somewhat modifies the developmental process in the later stages. (From Shull, Principles of Animal Biology.)*

Mesoderm Formation. In all but the two lowest phyla of the Metazoa, the completion of the diploblastic gastrula stage is immediately followed by the development of a third fundamental cell layer, the *mesoderm.* At this point, the similarity of development that is common to the embryos of all metazoans (except sponges) becomes less evident, and the embryos of various phyla begin to develop the diverse patterns of symmetry and organization that distinguish their respective groups.

Here we can consider only very briefly the mesoderm formation in Amphioxus and the frog.

In Amphioxus, gastrulation is accompanied by an elongation of the embryo, which is beginning to show bilateral symmetry. On either side of the middorsal line of the elongating (head to tail) axis of the body, the entoderm begins to evaginate (fold out) a linear series of connected pouches. These outgrowths become the mesoderm; they rapidly enlarge and are soon cut off from the entoderm tube, which "heals" together to show no traces of its former connection with the mesodermal pouches.

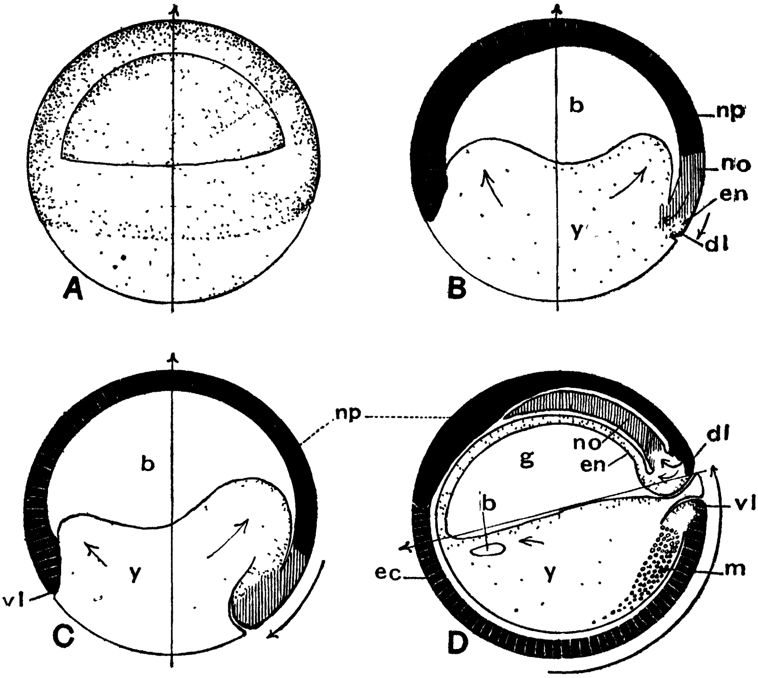

FIG. 96. *Schematized diagrams of gastrulation in the frog. (A) optical section of blastula; (B) beginning of gastrulation; (C) downward movement of dorsal lip of blastopore; (D) formation of archenteron and separation of notochord from entoderm.* **b**—*blastocoel;* **dl**—*dorsal lip of blastopore;* **ec**—*ectoderm;* **en**—*entoderm;* **g**—*archenteron;* **m**—*mesoderm;* **no**—*notochord;* **np**—*neural plate;* **vl**—*ventral lip of blastopore;* **y**—*yolk.*

The right and left mesodermal tubes grow rapidly and soon meet and fuse along the mid-ventral line of the embryo, thus completely separating the ectoderm of the outer body wall from the entoderm of the gut. The cavity of the mesodermal tubes forms the coelom, or true body cavity, which is thus lined with mesoderm and forms the outer space of the "tube-within-a-tube" body structure.

Mesoderm formation in the vertebrates is clearly comparable to that in Amphioxus, but it is usually modified or distorted, either by the yolk-laden condition of the entodermal cells or, in the case of the mammals, as a result of descent from ancestors that had such yolk-laden eggs.

The Primary "Germ Layers"

The ectoderm, entoderm and mesoderm constitute the so-called "primary" or "germ" layers, from which all the structures of triploblastic animals are developed. In all the higher metazoans, the differentiation of these layers constitutes but a very small fraction of embryonic development. By far the greater portion is occupied with the formation of the tissues, organs, and systems of the finished embryo from the derivatives and combinations of these primary tissues. In general, the outermost layers of the body, the nervous system, and the sensory parts of the sense organs are derived from ectoderm; the lining of the alimentary canal and its derivatives—liver, pancreas, lungs, etc.—are derived from entoderm; the contractile and sustentative portions of the skin and the digestive tract, the muscular, skeletal, circulatory, and excretory systems, and sustentative and contractile tissues as a group are developed from mesoderm.

Some Special Vertebrate Structures

Somite Formation. One of the fundamental devices of all vertebrate organization, the linear repetition of such structures as the vertebrae, ribs, spinal nerves, and certain blood vessels and thoracic muscles, is foreshadowed and determined by the early development of mesodermal *somites*. These are a linear series of paired, similar blocks that are formed as centers of condensation and more rapid growth in that part of the mesoderm that lies next to and on either side of the middorsal line of the embryo. The first pair of such centers forms on either side of what is to be the midbrain of the embryo, and the formation of additional centers proceeds rapidly backward (and slowly forward) from this point, each center contiguous to the one in front of it. This somite formation is so characteristic and regular that the number of somites that are visible at any given time gives one of the best indications of the stage in development reached by the early embryo, and much of the organization of the future body parts is a consequence of somite formation.

The Notochord. In Amphioxus and in all vertebrate embryos, the formation of a characteristic axial rod, the notochord, takes place at the same time as the formation of the mesoderm. In Amphioxus this rod is derived from the middorsal line of the entoderm by an evagination like that which produced the mesodermal pouches. The notochord, however, does not show any metameric arrangement into a linear series of pouches, nor does it develop a central cavity. It lies, as a cylindrical axial rod, dorsal to the alimentary canal. In the vertebrates (but not in Amphioxus), it is later replaced by the mesodermal tissues that form the centra of the vertebrae.

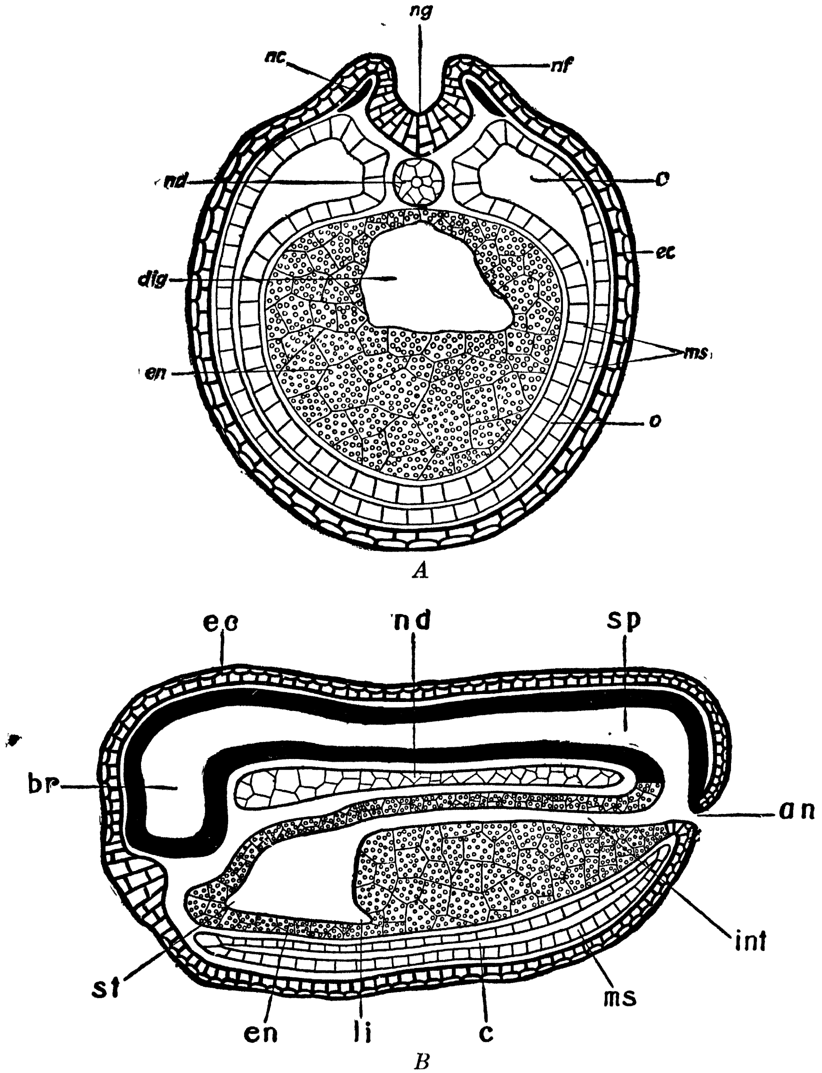

Fig. 97. *Diagrammatic cross (A) and longitudinal (B) sections through an early frog embryo. (an) Anus; (br) brain; (c) coelom; (dig) digestive tract; (ec) ectoderm; (en) endoderm; (int) intestine; (lc) lever; (ms) mesoderm; (nc) neural crest; (nd) notochord; (nf) neural fold; (ng) neural groove; (sp) spinal cord; (st) stomach. (From Shull, Principles of Animal Biology.)*

The Hollow Dorsal Neural Tube. Shortly after the beginning of the formation of the mesoderm and notochord, the development of the nervous system begins. The ectoderm along the middorsal line begins to grow rapidly, and a neural plate thicker than the rest of the ectoderm is formed. This development is most rapid in the region of what is to become the midbrain and progresses forward and backward from this point. The plate soon sags below the level of the remainder of the ectoderm and then folds, to form first a trough and then a tube that is cut off from the remainder of the ectoderm and lies beneath the outer ectoderm of the middorsal wall of the embryo, just above the notochord.

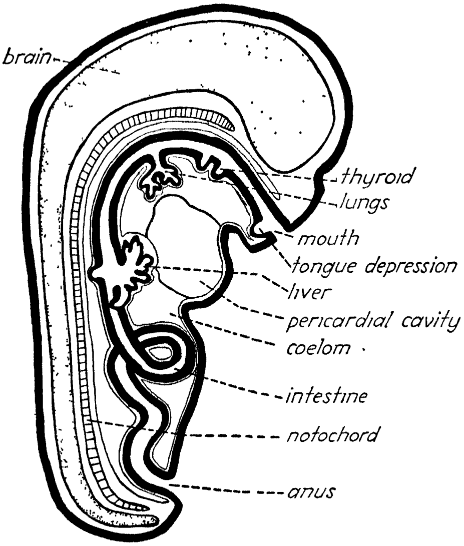

FIG. 98. *Diagram to show some developing structures in the chick embryo. A longitudinal section slightly to one side of the median line. (Redrawn from Shull, Principles of Animal Biology.)*

The rapid multiplication of the cells of the neural tube continues, and the tube soon develops a number of expansions that represent the early stages of the several brain regions. The longer portion of the tube posterior to the brain becomes the spinal cord.

The Gill Pouches. Another peculiar and universal feature of all vertebrate embryos is the formation of several pairs of gill pouches and gill arches. The side walls of the fore portion of the early embryonic gut, which forms at a very early stage in embryonic development, soon produce a series of paired (right and left) pouchlike outgrowths that extend toward the body wall of the neck region. At a slightly later stage, the outer body wall begins to grow inward in a series of lateral furrows, each furrow opposite the apex of an outwardly growing pouch.

The partitions between these paired pouches become regions of rapid mesodermal growth, and a series of alternating gill pouches and gill arches is soon formed on either side of the fore-gut. In the fishes and amphibians, the matched pouches and clefts soon unite (break through) to form *gill slits*, connecting the cavity of the fore-gut with the outside environment. In these groups, the gill arches become the supporting structures on which the gill membranes are developed and through which the blood vessels (aortic arches) run that connect the dorsal and ventral aortas. In the higher vertebrates—reptiles, birds, and mammals—the pouches and furrows do not completely break through, but they and the arches between them do profoundly modify embryonic organization and are variously utilized in the formation of subsequent adult structures.[1] The Eustachian tube, for instance, which connects our mouth cavity with the middle ear, is derived from the first (foremost) gill pouch; and our lower jaw, the cartilages that support our tongue, and our thyroid and parathyroid glands are derivatives of various other gill arches or pouches.

The Limb Buds. A fifth set of characteristic vertebrate structures, the paired pectoral and pelvic limbs, also make their beginning in early embryonic life. The paired buds that are to develop into the pectoral girdle and forelimbs are the first to appear. They arise as lateral protuberances that show a very rapid growth, involving several of the paired somites and associated tissues in the shoulder region. The buds that are to form the hind limbs are markedly similar except for their more caudal (tailward) position and their at first more retarded development.

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[1] The aortic arches of the various vertebrate groups owe their arrangement to that of the early embryonic gill arches, and our own pulmonary arteries and several of the important branches from the basal part of our aorta are derived from the embryonic blood vessels that traversed these arches.

CHAPTER XVIII

Reproduction in Plants

Although the reproductive processes of plants are fundamentally similar to those of animals, certain striking differences occur.[1] In animals, we found it convenient to differentiate between reproduction in unicellular and in multicellular forms and to base our classification of metazoan reproduction upon the distinction between germ and soma. In plants, the distinctions between unicellular and multicellular and between germ and soma are much less clear-cut, and other criteria have been adopted for the classification of reproductive processes.

The Alternation of Generations. Except for the most primitive forms, the typical life cycle of any plant includes two stages or generations—a *haploid gametophyte* generation, which reproduces sexually by gametes, and a *diploid sporophyte* generation, which reproduces asexually by means of spores. Here sexual reproduction involves the fusion of two gametes to form a diploid zygote, which develops into a sporophyte individual, and asexual reproduction involves the formation of minute haploid cells, which develop into gametophyte individuals.[2]

Simple Vegetative Reproduction. In addition to the reproductive processes that are associated with the alternation of generations, nearly all plants are capable of a direct and clearly asexual vegetative reproduction. By a process that is essentially like the budding or fission of the lower metazoans, individuals of the gametophyte generation may produce other gametophyte individuals, and individuals of a sporophyte generation may produce other sporophyte individuals. In many plants, both high and low, this direct vegetative process forms an important or even the chief method of reproduction.

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[1] Among multicellular forms, the divergence in the plants' and the animals' ways of life has involved their reproductive practices. At least a part of the difference appears to be due to the fact that nearly all the nonmotile plants have utilized reproduction to provide for the dispersal of their progeny.

[2] This is perhaps the most fundamental difference between the reproductive cycles of the Metazoa and the multicellular plants. In the Metazoa, the haploid stage is confined to the unicellular gametes (sperm and egg), which immediately unite to form a zygote; in plants, the reduction division takes place at spore formation, and the haploid cells have a more or less prolonged existence as an often long-lived gametophyte generation.

REPRODUCTION IN THE THALLOPHYTES

We have seen that the thallophytes include the algae, fungi, and bacteria and form the lowest of the four great groups of the plant kingdom. In this group, we not only find the most primitive of all types of reproduction but also encounter a graded series of reproductive processes that appear to include the origin both of sex and of the alternation of generations.

Reproduction by Simple Fission. In the blue-green algae, in the bacteria, and perhaps in some of the most primitive fungi, the protoplasm of the cells shows little or no differentiation. Here reproduction is by the simplest type of fission and does not even involve mitotic processes. In some of the lowest of the green algae, in which the protoplasm is differentiated into nucleus and various cytoplasmic structures, all reproduction is still by fission, but by a fission that now involves mitosis.

Budding in yeasts differs from fission in that the parent cell produces a small bud that gradually grows to full size without the parent cell losing its identity but is like fission in that a single yeast cell is able to produce a daughter cell without a stimulus from another individual.

Sexual Reproduction in the Thallophytes. In the great majority of the green algae, reproduction is not confined to fission, although this still forms the chief method for the rapid multiplication of individuals and colonies during the growing season. From time to time, however, usually in response to unfavorable environmental conditions, two alga cells fuse to form a zygote, which, after a resting season, will reproduce new individuals or a new colony. Here considerable variations occur. In some species, the two cells that fuse are indistinguishable from any of the other vegetative cells and from each other. In other species, the fusion cells are more or less specialized. They may be alike—small, motile cells, *isogametes*, that are formed by the division of larger vegetative mother cells; or they may be differentiated into two types of gametes—small, motile, spermlike *microgametes* and larger, nonmotile, egglike *macrogametes*. In any event, the two cells that fuse—whether they be undifferentiated vegetative cells or isogametes or microgamete and macrogamete—are haploid, and the resulting zygote is diploid.

In the thallophytes, the diploid condition is restricted to the zygote.[1] At the first cell division, the zygote undergoes a reduction division and so produces only haploid daughter cells.[1] Here we have not only the beginnings of sex in plants but, in the diploid zygote stage, a foreshadowing of the alternation of generations.

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[1] Except in certain of the higher algae.

Reproduction in Thallophytes in General. The algae and fungi show a wide range in structure, size, and appearance and have been variously modified for many types of life. The details of their reproductive processes are correspondingly varied but may be grouped into three main types:

1. *Simple vegetative reproduction,* both in unicellular forms, such as the bacteria and certain algae, and in many multicellular algae and fungi, where fragments of alga filaments or fungus mycelia grow into new filaments and mycelia.
2. *Spore formation,* which may be subdivided into two types: the typical sporulation that follows the production of the diploid zygote, and a type of spore formation that results from the rapid and repeated division of a spore mother cell that was developed from haploid vegetative tissues without fertilization.
3. *Sexual reproduction,* which always involves the fusion of two gametes to form a zygote.

THE ALTERNATION OF GENERATIONS IN THE BRYOPHYTES

In the mosses and liverworts, which make up the second great subdivision of the plant kingdom, an alternation of gametophyte and sporophyte generations is clear-cut and unmistakable. The gametophyte generation forms the more conspicuous part of the life cycle and is represented by the small green "leafy" plants that we recognize as mosses[2] or liverworts; but a sporophyte generation is now invariably a part of the cycle.

Sexual Reproduction in the Mosses. When the leafy stem of the gametophyte individual has reached its full growth, the upper end produces many-celled sex organs of two kinds. The female sex organs (*archegonia*) become vaselike in shape, and one of the cells near the bottom of the vase develops into a large egg. The male sex organs (*antheridia*) produce a huge number of ciliated male gametes or sperms. These, when released from the antheridium, are able to swim in water films provided by rain and dew and so reach the egg within the female sex organ. The union of a male gamete with the egg produces a diploid zygote that develops into a diploid sporophyte plant. This sporophyte generation is not free-living but lives as a parasite on the green gametophyte. It forms a bulblike *foot* that grows down into the gametophyte tissues to obtain nourishment, and then sends up a stalklike structure that develops a conspicuous capsule at its distal end. The foot, stalk, and capsule, which lack chlorophyll and are usually somewhat longer than the leafy gametophyte stem from which they extend, constitute the sporophyte generation that begins with the zygote.

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[1] In some green algae, the first division of the zygote produces two vegetative cells that continue to multiply by fission; in other species, two or more consecutive divisions result in the production of small haploid spores, each capable of giving rise to a new vegetative colony or individual.

[2] "Spanish moss," so common a sight in the South, is not a moss at all but a flowering plant (spermatophyte), related to the air plants and the pineapple.

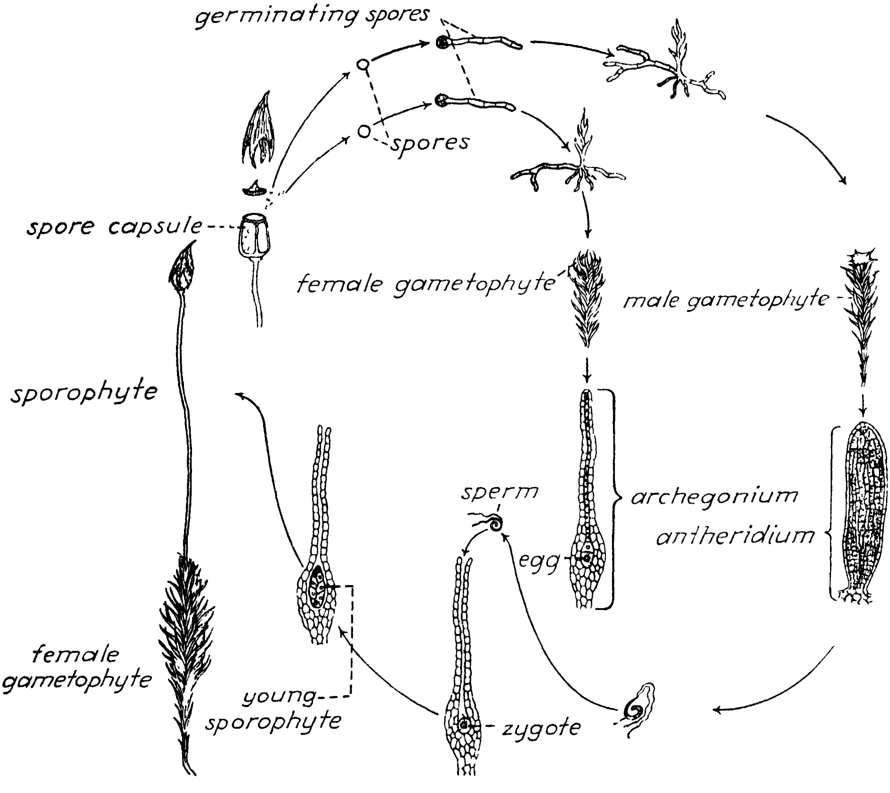

germinating spores
spores
spore capsule
female gametophyte
male gametophyte
sporophyte
sperm
archegonium
antheridium
egg
female gametophyte
young sporophyte
zygote

FIG. 99. *Alternation of generations in the Bryophytes. The life cycle of a moss. (Courtesy of the General Biological Supply Company.)*

Spore Formation. Once the sporophyte tissues are complete, spore mother cells within the capsule undergo maturation and repeated asexual divisions to form a large number of haploid spores. The ripe spores, when discharged from the capsule, may fall near by or be carried a considerable distance by the wind. Those that chance to alight in a favorable environment absorb water and germinate to produce new gametophyte individuals.

THE ALTERNATION OF GENERATIONS IN THE PTERIDOPHYTES

In the ferns—and their relatives, the club mosses and horsetails—we find the most striking alternation of generations that occurs among plants. It is now the sporophyte generation that is the more accentuated and conspicuous, so that the plants we recognize as ferns, club mosses, or horsetails are members of the sporophyte generation. The gametophyte generation is here reduced to small but free-living plants that persist only long enough to give rise to a new sporophyte generation.

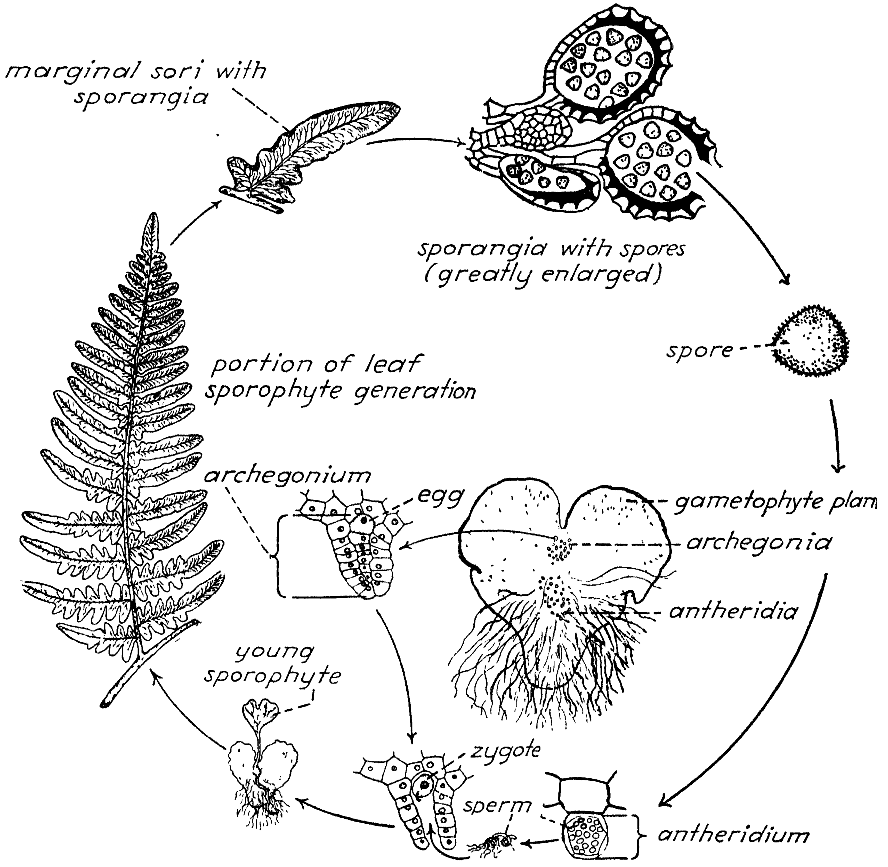

marginal sori with sporangia
sporangia with spores (greatly enlarged)
spore
portion of leaf sporophyte generation
archegonium
egg
gametophyte plan
archegonia
antheridia
young sporophyte
zygote
sperm
antheridium

FIG. 100. *Alternation of generations in the Pteridophytes. The life cycle of a fern.* (*Courtesy of the General Biological Supply Company.*)

Spore Formation. On the backs of the fronds of many ferns, one may often observe small fruit dots or sori. These are composed of numerous minute spore cases, or *sporangia*, in which are contained a number of spore mother cells. These cells undergo reduction and division to form spores that, when ripe, are thrown into the air by the violent bursting of the sporangium.

The Gametophyte Generation. Such of the spores as chance to fall into favorable situations soon germinate. The spore wall cracks open, and the protoplasmic contents undergo repeated cell divisions that result in the production of a small, green, flat, somewhat heart-shaped structure known as the *prothallus*, which constitutes the gametophyte generation. Except for the region of the marginal notch, the prothallus is but one cell thick. It produces a number of threadlike structures (*rhizoids*) on its lower surface, which extend into the soil, where they take up water and salts.

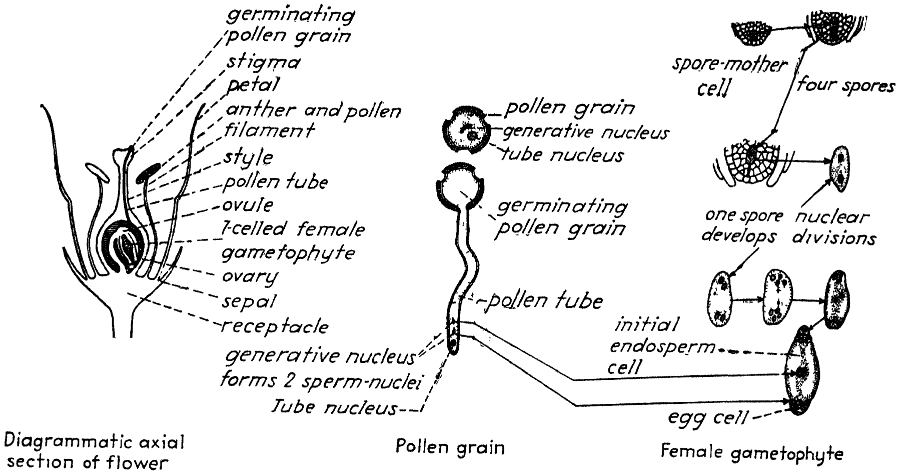
Sexual Reproduction. The sex organs are borne on the lower surface of the prothallus. The female sex organs, or archegonia, are flask-shaped and are borne in the region of the thickened marginal notch. Each archegonium contains a single egg at the bottom of the open-mouthed flask. The male sex organs, or antheridia, are more or less spherical in shape and are smaller than the archegonia; they are located near the apex of the "heart." A number of sperms are formed within each antheridium. When a ripened antheridium becomes wet with rain or dew, it swells and bursts, thus allowing the sperms to escape. The latter swim through the water film to the archegonia, which they enter by way of the open mouths. Within an archegonium, a single sperm fuses with the egg to form a zygote.

The Development of the Sporophyte. The zygote begins its development within the walls of the archegonium and soon forms definite structures of its own: a "foot" that enables the developing embryo to absorb nourishment from the prothallus, and an embryonic root, stem, and leaves. By the time the latter have become functional, the prothallus shrivels, and the young sporophyte is left dependent upon its own tissues for maintenance.

THE ALTERNATION OF GENERATIONS IN THE SPERMATOPHYTES

In the seed plants, which constitute the fourth and highest division of the plant kingdom, the alternation of generations has become largely concealed by an increased emphasis on the sporophyte generation and the reduction of the gametophyte generation to a brief parasitic existence within the tissues of the sporophyte. Although the cycads and the familiar conifers and flowering plants, which together constitute the spermatophytes, are distinguished by marked differences in the details of reproductive adaptations, a consideration of reproduction in the flowering plants will illustrate all the essential points in the alternation of generations within the spermatophytes.

The Gametophyte Tissues of the Flowering Plant. We have already seen something of the structure of a typical flower and learned that it consists of four sets of floral parts that are arranged concentrically. Here we are concerned with the two inner sets of parts—the *stamens* and the *pistil,* or *pistils*—for these are the sporophyte organs within which spore formation will result in the production of a haploid gametophyte generation. Spore formation gives rise to two types of spores—small spores (*microspores*), which will form the pollen grains; and large spores (*macrospores*), which, together with the thick-walled spore case, constitute the "ovules" of the flower.


germinating pollen grain
stigma
petal
anther and pollen
filament
style
pollen tube
ovule
7-celled female gametophyte
ovary
sepal
receptacle
pollen grain
generative nucleus
tube nucleus
germinating pollen grain
pollen tube
generative nucleus forms 2 sperm-nuclei
Tube nucleus
spore-mother cell
four spores
one spore develops
nuclear divisions
initial endosperm cell
egg cell

Diagrammatic axial section of flower

Pollen grain

Female gametophyte

FIG. 101. *The gametophyte generation of a spermatophyte. The separate male and female gametophytic plants are formed in the anther and ovary of the flower respectively, and the female gametophyte continues to develop parasitically in the sporophyte tissues of the ovary until it forms a seven-celled structure, one of the cells being the ovum and the large central binucleate cell the beginning of the endosperm tissues. (Courtesy of the General Biological Supply Company)*

Microspores and Pollen. The anther that forms the apical end of each stamen is in reality a spore case, though we conventionally speak of it as the male organ of a flower. Within the anther, a large number of spore mother cells are formed, which undergo a maturation process in the course of which each spore mother cell produces four haploid microspores. These are destined to become the pollen grains, and, indeed, so far as any external appearances are concerned, there is nothing to distinguish them from mature pollen grains, even at this stage. Before they are ready to fertilize the egg, however, they must undergo a series of internal changes, which can best be understood if we briefly review the concept of alternation of generations in the plant. The microspore is an asexual reproductive body which, in the lower groups of plants, would germinate into the haploid male gametophyte; this would, in turn, produce the haploid male germ cell, and the latter would effect fertilization and the return to the diploid condition.

The equivalents of these steps do actually occur in the flowering plants, but in such compact, reduced form that they are hard to recognize. The microspore "germinates" within its own spore case by nuclear division unaccompanied by any cytoplasmic division. The first nuclear division produces two nuclei, one called the *tube nucleus,* which may be regarded as somatic, and the other called the *generative nucleus,* which may be regarded as a germ cell. The generative nucleus then proceeds to divide once more, giving rise to two nuclei which function as male gametes and which are called the *sperm nuclei.* At this stage, the entire structure has become a mature pollen grain and may be regarded as a minute male gametophyte consisting of one vegetative cell and two germ cells. These changes normally take place in the anther before the pollen is shed and occur within the original microspore case, which accounts for the confusion that sometimes arises over the distinction between microspores and pollen.

Macrospores and the Female Gametophyte. The female spores, or macrospores, are produced within the swollen base of the pistil, known as the *ovary.* Here, within the cavity of the ovary, one or more female spore cases, or "ovules," are formed. Each ovule or spore case, unlike the spore cases of the mosses and the ferns, is a thick-walled structure, composed of several layers of cells, which contains a single large spore mother cell. The latter undergoes a maturation process very like that of the metazoan egg and produces a single large macrospore. This spore now germinates within the ovule and grows into a gametophyte that consists of a cytoplasmic mass with four nuclei at either end. One nucleus from each group of four next migrates to the center of the mass, where they will later fuse to form the *primary endosperm nucleus.* One of the three nuclei that remain at the end of the gametophyte nearest the opening of the ovule then grows much larger than the rest and together with a portion of the cytoplasm becomes enclosed with a cell membrane to form a single egg.

Further development of the egg is dependent upon three processes: (1) *pollination,* or the transfer of pollen grains from an anther to the stigma of the pistil; (2) *germination of the pollen grain* on the stigma and its growth down the style of the pistil to the ovule; and (3) *fertilization* of the egg and of the primary endosperm nucleus by sperms from the pollen tube.

Methods of Accomplishing Pollination. We have seen that in the metazoa, bisexual reproduction is dependent upon some appropriate behavior of the parent organisms that brings the motile sperms within a short distance of the egg. Although the lower plants have male gametes that are motile and are capable of swimming short distances to meet the egg, in the flowering plants the pollen grains lack any means of locomotion and must be passively carried to the stigma.

Self-pollination. In contrast to the rarity of self-fertilization among the Metazoa, self-pollination is, for a number of important groups of plants, a normal and almost invariable process. In the bean or pea, for example, the anthers and stigma are enclosed within the other floral parts, and pollination is accomplished by the pollen falling directly from the ripe anthers to the stigma. In other self-pollinating flowers, a properly timed growth of the pistil thrusts the ripe stigma against the anthers as they open to expose the pollen grains.

Cross-pollination. In a large majority of the flowering plants, cross-pollination is the rule, and here some other agent than gravity or the growth of the pistil must be utilized. In most flowers, this is effected by animal visitors. The flowers are specially adapted to attract such visitors by having nectaries that secrete a sweet fluid called *nectar* and by producing quantities of pollen in excess of their own needs. Bees are the commonest pollinating agents, but other animals such as hummingbirds, butterflies, moths, beetles, and certain other insects also play a part. Almost all flowers that are not insect-pollinated are wind-pollinated; they produce vast quantities of pollen, which is broadcast in the air and reaches its destination solely by chance. The grasses are the largest group of flowering plants making use of this method.

Development of the Seed. The "double" fertilization stimulates both the egg and the tissues of the endosperm and ovule to active growth. The fertilized egg, by rapid cell divisions, comes to form the embryonic plant, already described in a previous section; the endosperm becomes greatly swollen with stored food for the use of the growing embryo; and the walls of the ovule itself become thick and tough to form the resistant outer coats of the seed. The seed may thus grow to be hundreds of times the size of the ovule before fertilization. In many dicotyledons, such as the bean, by the time the seed is mature the embryo has absorbed all the food originally stored in the endosperm and has, in turn, stored this food in its own much enlarged cotyledons. In other plants, such as corn, wheat, and all other grasses, the embryo forms a relatively small part of the mature seed, most of which is made up of the endosperm. The structure of seeds and of fruits has already been discussed in Chap. XIV.

CHAPTER XIX

Mendel's Laws of Inheritance

THUS far we have taken for granted that the new individuals of each generation will be like the parents that produced them and that the peculiar characters by which we distinguish one race from another will be perpetuated. Generally speaking, this is true, and the realization of its truth has given rise to such proverbs as "like begets like" and such metaphors as "a chip off the old block" and such folklore stories as that of the ugly duckling. The biologist has also recognized the general truth of "like begets like" in his definition of a kind or *species* of organism as "a group of like individuals that naturally perpetuate themselves by reproduction." Nevertheless, it is easily seen that offspring are not exact duplicates of their parents. Only very rarely is it difficult to see well-marked differences between full brothers, or full sisters; some children appear to "take after their father"; others "take after their mother"; some are intermediate or are not very like either parent. Yet we do not hesitate to say that, on the whole, like does beget like.

We are here encountering two apparently contradictory phenomena that have been termed *heredity* and *variation.* By heredity is meant the passing of like qualities from one generation to the next. Many of these qualities are common to all the members of the race; others, not common to all the race, are likely to be common to or very frequent in a given parent-offspring sequence within that race. By variation, on the other hand, we mean all departures from a complete identity of qualities—the differences that permit us to distinguish between two individuals of the same race or of the same parent-offspring sequence.

The practical breeder, convinced of the general truth that like begets like, has long utilized these phenomena of heredity and variation. Selecting the most desirable variants from a litter, a herd, or a crop, he has utilized them for the parents of the next generation, eliminating less desirable individuals from the reproductive sequence. This process, repeated generation after generation, has led to the development of many distinct breeds of domesticated animals and plants, each characterized by the accumulation into a common inheritance of a desirable combination of formerly more variable qualities, and the elimination of other (undesirable) qualities that had regularly or frequently appeared in the original ancestral stock. One has only to consider some of the many existing breeds of dogs, cattle, poultry, corn, or tobacco to realize how effective such a practical manipulation of variation and inheritance has been.

Until the present century, however, the work of the practical breeder, although extremely productive, had been almost wholly empirical and by "rule of thumb," and the plight of the biologist was little if any better, in spite of the accumulation of much careful data from observation and experiment. Then, in 1900, with the rediscovery of Mendel's long-neglected pioneering work, the biologist was given a sound foundation and a powerful research method for the investigation and understanding of inheritance and variation.

Gregor Johann Mendel was an Augustinian monk and later the prelate or abbot of a monastery in Brünn (now Brno), Austria. In 1865, after 8 years of thorough study, he announced the results of his work on the inheritance of certain qualities in the garden pea. Many other workers before his time had made somewhat similar investigations, but Mendel's experiments were so carefully thought out and so painstakingly made and recorded that he was able to discover underlying principles of inheritance that could not have been disclosed by less precise methods. His procedure (which was to become one of the fundamental tools for modern genetic studies) is so important that it is necessary to describe it in some detail.

The Selection of Experimental Material. At the beginning of his studies, Mendel obtained as many varieties of peas as he could find. He tested each variety by growing it for several generations and then selected several that differed from each other in one or more distinct characteristics and that proved to breed true. For example, he obtained one variety in which all the individuals were tall (5 to 6 feet) and another in which all the individuals were dwarf (18 inches to 2 feet); a variety with smooth seeds and another with wrinkled seeds; a variety in which the seeds were always green and another in which the seeds were always yellow; etc.

THE MONOHYBRID CROSS

Mendel's simplest experiments were concerned with crosses between varieties that differed from one another in a single definite quality. One of these was the cross between the tall and the dwarf varieties. The garden pea is normally a self-fertilizing species, so that Mendel's first step was to select one plant—a tall one, for example—and remove all its anthers before the pollen was ripe. The plant was thus completely emasculated and incapable of fertilizing itself. When the stigmas of this plant were ready for pollination, he introduced pollen from the anthers of the dwarf variety and so effected a cross between the two varieties. The cross-pollinated flowers of the tall plant were then protected against the entrance of other pollen and allowed to mature their seeds.

The Offspring (F_1) of the Monohybrid Cross. Mendel planted the seeds produced by crossing the tall and dwarf varieties, and when they were grown, all the plants were fully as tall as the tall parent and none resembled the dwarf parent. These tall offspring were allowed to self-fertilize and produce seed without interference.

The F_2 ("Grandchildren") of the Monohybrid Cross. When the seeds from the F_1 generation were planted, they produced an F_2 (or grandchild) generation that consisted of both tall and dwarf plants. When Mendel counted the number of tall and of dwarf individuals in this generation, he found that approximately $3/4$ were tall and approximately $1/4$ were dwarf.

Repetition of the same experiment gave the same results. Mendel found that it made no difference whether he took the pollen from the dwarf variety and placed it on the stigmas of the tall variety or took pollen from the tall variety and placed it on the stigmas of the dwarf variety. In all cases, the immediate offspring, the F_1, were all tall, and the grandchildren, the F_2, were approximately $3/4$ tall and $1/4$ dwarf. Further, he discovered that if he planted all the seed produced by the dwarf plants of the F_2, they would produce only dwarf plants. When, however, he planted the seeds produced by the tall plants of the F_2, he found that the seeds from approximately one-third of these tall plants produced only tall plants but that the seeds from the other two-thirds produced, on the average, $3/4$ tall plants and $1/4$ dwarfs.

Mendel then made similar crosses between other varieties that showed contrasted qualities. A cross between the yellow-seeded and green-seeded varieties produced only yellow-seeded individuals in the F_1 generation and a ratio of $3/4$ yellow-seeded and $1/4$ green-seeded, in the F_2 generation. Another cross, that between the wrinkled-seeded and round-seeded varieties, produced an F_1 that were all round-seeded and an F_2 that were $3/4$ round-seeded and $1/4$ wrinkled-seeded.

In all, seven sets of contrasted characters were found and crossed, and all the crosses showed a number of features in common:

1. In all crosses, the original parents were from varieties that, until crossed, invariably bred true to the quality in question.

2. The crosses were all between varieties that differed from each other in regard to one particular pair of characters: tall versus dwarf, yellow versus green, round versus wrinkled, etc.

3. The members of the F_1 generation *were all alike* and resembled one of the parents to the exclusion of the other.

4. The members of the F_2 generation were always of two sorts, approximately ¾ like the F_1 and the parent that the F_1 resembled, approximately ¼ like the other member of the original parent cross.

5. The smaller group (the ¼) of the F_2 generation would breed true if allowed to self-fertilize; approximately only one-third of the larger group (the ¾) of the F_2 would breed true, the other two-thirds again giving a ¾:¼ ratio of the same contrasted qualities.

It seemed evident that some basic principle was common to all these crosses, and Mendel now sought to discover what this basic principle might be. He assumed that each individual must have two factors for each quality but that a germ cell produced by the individual could carry but one factor from any pair present in the individual. It would follow, then, that factors would be separated at germ-cell formation and united into pairs at fertilization.

We can diagram this idea, using the cross between the tall and dwarf peas, by letting the capital letter *D* represent the factor for tallness and the small letter "*d*" represent the factor for dwarfness (which, as we have seen, acts as an alternative to tallness in inheritance in peas). (Mendel's original notation is here slightly changed to make it conform to modern usage.)

The following diagram shows that Mendel's hypothesis fits all the observed facts:

Diagram of Monohybrid Cross

The original parent generation P_1	Tall	×	dwarf
Gene formula of P_1	*DD*		*dd*
Formulas of gametes produced by each parent..	*D*		*d*
Resulting formula of F_1 generation............		*Dd*	
	(All tall, all alike)		

Gametes produced by each F_1 individual (two kinds in equal numbers)	*D* and *d*			
Union of gametes to produce F_2 zygotes, when F_1 is self-fertilized or interbred	Female gametes	*D*	*d*	
	Male gametes	*D*	*d*	
		DD	*Dd*	
Probable proportion of all possible combinations			*dD*	*dd*
		DD	(2)*Dd*	*dd*

The F_2 generation........................ $\underbrace{\text{1 tall } (DD)\text{—2 tall } (Dd)}_{\text{3 tall}}\text{—}\underbrace{\text{1 dwarf } (dd)}_{\text{1 dwarf}}$

1. Each of the original parents (P_1 generation) has both factors alike, *DD* or *dd*, because it came from a variety proved to breed true for its respective quality.

2. As a consequence, any germ cell produced by the tall parent could only receive a *D*, and any produced by the dwarf parent could only receive a *d*.

3. The cross must bring together a gamete with *D* and a gamete with *d*, and the resulting zygote that develops into an F_1 individual must have the formula *Dd*. (Since the individuals of the F_1, with the formula *Dd*, are as tall as the original tall parent with the formula *DD*, *D* is said to be *dominant* to *d*, and tall is said to be *dominant* to dwarf.)

4. When an F_1 individual produces its germ cells, there will be two kinds in equal numbers, *D* and *d*. This will apply to the formation of both pollen and ovules.

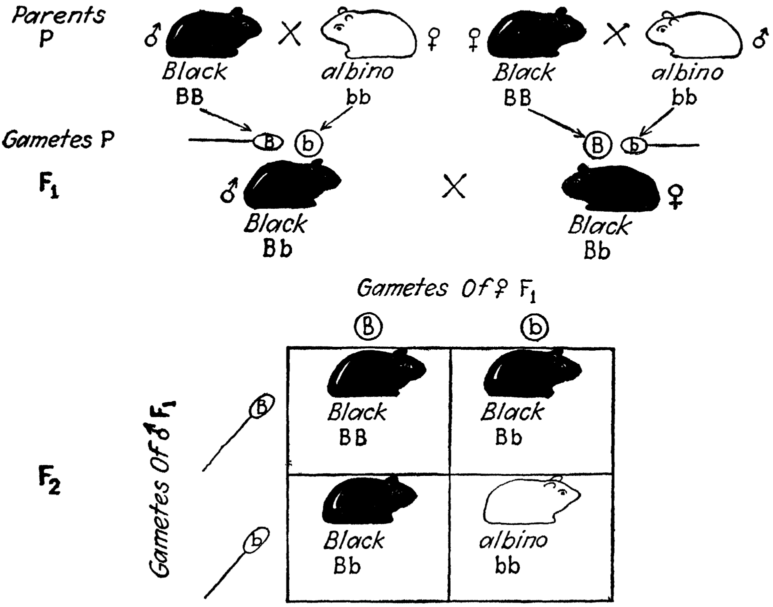


FIG. 102. *Diagram showing the results of crossing two guinea pigs differing by one character and each homozygous for that character, and the checkerboard showing the results in the F_2 generation. (From Wolcott, Animal Biology.)*

5. Since half of the female gametes are *D* and half *d* and since half of the pollen grains are *D* and half *d*, there are four possible ways in which they can combine: (1) pollen *D* with ovule *D—DD*; (2) pollen *D* with ovule *d—Dd*; (3) pollen *d* with ovule *D—dD*; and (4) pollen *d* with ovule *d—dd*.

6. According to the laws of chance, the resulting combinations should be in the following proportions: $\frac{1}{4}DD$, $\frac{2}{4}Dd$, and $\frac{1}{4}dd$. Since, as

we have seen in paragraphs 1 and 3, above, both *DD* and *Dd* produce an equal degree of tallness in the individual, ¾ of the F_2 should be tall and ¼ dwarf.

7. It is also evident that all the dwarf members of the F_2 should breed true but that only one-third (the *DD* individuals) of the talls should breed true; the other two-thirds of the talls (the *Dd* individuals) should produce a ¼*DD*, 2/4*Dd*, and ¼*dd* ratio when allowed to self-fertilize.

Here, then, is a hypothesis that explains all Mendel's monohybrid crosses. If we make exactly the same assumptions and diagram the cross between yellow-seeded (*GG*) and green-seeded (*gg*) peas, or the cross between round-seeded (*WW*) and wrinkled-seeded (*ww*) peas, we see how it comes about that they produce the same numerical ratios in the F_1, F_2, and subsequent generations.

MENDEL'S FIRST LAW: GAMETIC PURITY

The principle of inheritance that has just been discussed is now known as *Mendel's first law* and is often stated as follows: "Inherited pairs of factors segregate at germ-cell formation and recombine at fertilization." The first law is often referred to as the *principle of gametic purity, i.e.*, that a gamete can carry but one of any two alternative characters (for example, *D* or *d*) and hence can never be hybrid. It is also important to note that neither the *D* nor the *d* produced by the hybrid F_1 generation is in any way contaminated by their existence together in the F_1 generation and that each is just as "pure" as if derived from pure-breeding tall and dwarf individuals, respectively.

SOME NECESSARY TERMINOLOGY

In order to follow Mendel's further work, as well as post-Mendelian genetics, it is necessary to learn a number of definitions and time-saving genetic conventions and symbols. These not only make for greater clarity and preciseness but save much time in writing and thinking about genetic concepts.

gene (***factor*** or ***determiner***). An unknown entity carried in the germ cells that (under proper conditions) results in the development of a definite quality by the zygote. (The term *gene* is generally preferable to the synonymous terms *factor* and *determiner*.)

allelomorph or ***allele***. One of a pair of genes or characters that are contrasted in inheritance. Tall and dwarf are examples of allelomorphic characters; *D* and *d*, of allelomorphic genes. The term is applied to both characters and genes, but characters that are not inherited as alternatives are not allelomorphic.

gamete. A germ cell, either male or female. As used in genetics it applies to spermatozoa, ova, pollen, and ovules.

gametic formula. The formula of a gamete in terms of the genes it is known to carry. Because of the principle of gametic purity, a gamete can have but a single gene from any allelomorphic pair. Examples: d, D, Ab, AbC, abC, etc.

zygote. The product of the union of two gametes. By extension, it is also applied to the individual that is produced by the development of a zygote and is used in opposition to the haploid gamete.

zygotic formula or ***zygotic constitution.*** The formula for a zygote or individual that it, he, or she is known to carry. Examples: dd, DD, Dd, $Aa\ BB\ cc$, etc.

homozygote. An individual with like genes for the pair or pairs under consideration. Examples: DD, dd, $AA\ bb$, etc.

heterozygote. A zygote or individual with unlike genes for the pair or pairs under consideration. Examples: Dd, $Aa\ Bb$, etc. NOTE: an individual may be homozygous for some genes and heterozygous for others. Example: $AA\ Bb$.

hybrid. The result of a cross of unlike parents, a heterozygote.

monohybrid. A cross that involves but a single pair of contrasting genes. Sometimes applied to the F_1 product of such a cross.

dihybrid. A cross that involves two pairs of contrasting genes.

trihybrid. A cross that involves three pairs of contrasting genes

genotype. The description of an individual in terms of the genes that he, she, or it is known to possess.

phenotype. The description of an individual in terms of its visible characters. Tall is a phenotypic description, in the pea, and may be due to either of two genotypes, DD or Dd.

P_1. The original parent generation; typically consists of a male and female that are each homozygous and differ in regard to one or more pairs of contrasting genes.

F_1. The first filial generation, the immediate offspring of the P_1; always all alike and all hybrid.

F_2. The second filial generation, the offspring of F_1 individuals, and the generation that shows various diagnostic phenotypic ratios.

THE DIHYBRID CROSS

Mendel's studies did not stop with the making and analyzing of monohybrid crosses. His experiments also included several dihybrid and trihybrid crosses that resulted in the discovery of a second great principle of inheritance. We shall examine one of these crosses in detail.

Among the varieties at Mendel's disposal was one in which the ripened seeds were round in shape and had a yellow color; another variety had seeds that, when ripe, were shriveled or wrinkled and retained their green color. The cross between these varieties was effected precisely as was the one between tall and dwarf—the pollen from an individual of one variety was transferred to the stigmas of an individual of the other variety and so produced a cross-fertilization.

The Dihybrid F_1. The F_1 seeds were all yellow and round, as we should expect from the results already given for monohybrid crosses between round and wrinkled and between yellow and green.

The Dihybrid F_2. On planting the F_1 seeds and allowing the flowers produced by them to self-fertilize, Mendel obtained four kinds of seeds—

yellow and round, yellow and wrinkled, green and round, and green and wrinkled. Here were not only the original parent types—yellow and round and green and wrinkled—but also *two new combinations*—yellow and wrinkled and green and round. When the number of each of the four types was counted, it was found that 315 were yellow and round;

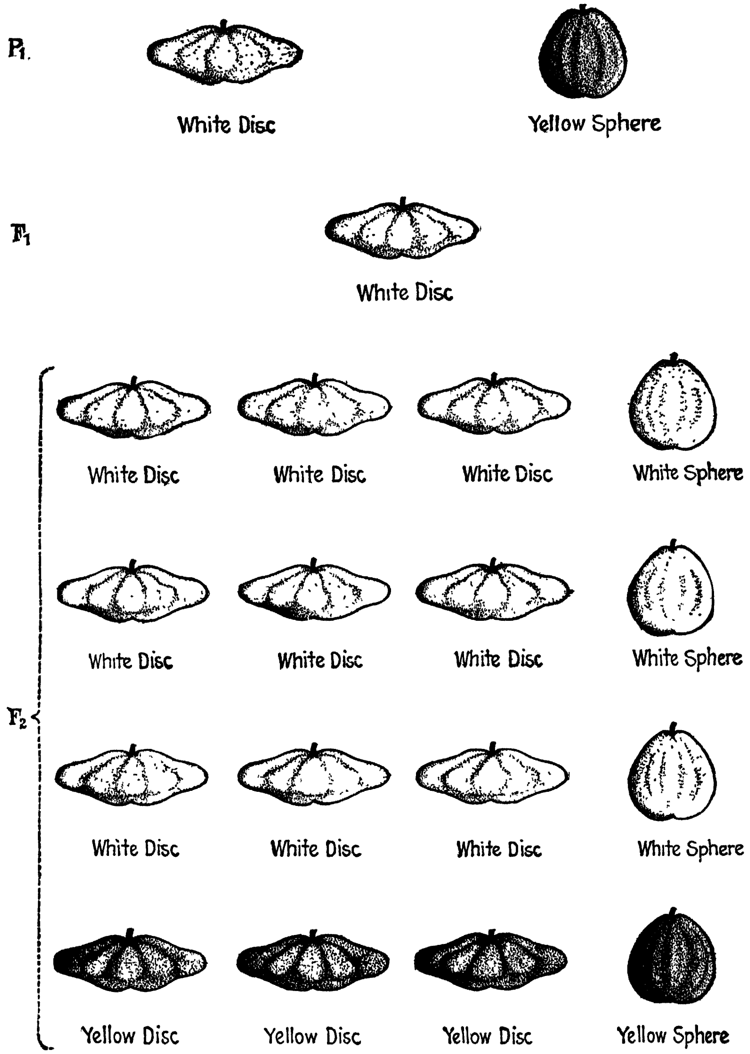

P1.
White Disc
Yellow Sphere
F1
White Disc
White Disc
White Disc
White Disc
White Sphere
White Disc
White Disc
White Disc
White Sphere
F2
White Disc
White Disc
White Disc
White Sphere
Yellow Disc
Yellow Disc
Yellow Disc
Yellow Sphere

FIG. 103. *The dihybrid cross between white disc and yellow sphere in the summer squash. White is dominant to yellow and disc is dominant to sphere. The F_2 ratio shows that the segregation of the genes for white and yellow must have been independent of the segregation of the genes for disc and sphere.* (*From Sinnott and Dunn, Principles of Genetics.*)

101 were yellow and wrinkled; 108 were green and round; and 32 were wrinkled and green. The proportion of yellow to green is (315 + 101): (108 + 32), approximately $3/4 : 1/4$; and the proportion of round to wrinkled is (315 + 108):(101 + 32), again approximately $3/4 : 1/4$; but how are we to account for 101 individuals that are yellow and wrinkled and 108 that are green and round?

MENDEL'S SECOND LAW: INDEPENDENT ASSORTMENT

Mendel saw that the two new combinations—yellow and wrinkled, and green and round—could be accounted for if he assumed that segregation between the genes for yellow and green was *independent* of the segregation that takes place between the genes for round and wrinkled. That is, although the hybrid F_1 received its genes for yellow and round from one gamete and its genes for green and wrinkled from the other, these genes would not tend to stay together when the F_1 generation formed its germ cells. Such independence in segregation would result in the F_1 individuals forming four kinds of male and female gametes in equal numbers:

1. Containing a gene for yellow and a gene for round.
2. Containing a gene for yellow and a gene for wrinkled.
3. Containing a gene for green and a gene for round.
4. Containing a gene for green and a gene for wrinkled.

If one of each of the four types of male gametes then fertilized one of each of the four types of female gametes, four classes of phenotypes should be produced, in the proportion of $9/16$ that are yellow and round, $3/16$ that are yellow and wrinkled, $3/16$ that are green and round, and $1/16$ that are green and wrinkled.

This can be more clearly expressed if we use a diagram to describe the various individuals and germ cells involved. We have already used *W* to represent the gene for round and *w* to represent the gene for wrinkled; *G* to represent the gene for yellow and *g* the one for green. Consequently, the genetic formula for the two P_1 individuals may be written *GG WW* for the yellow-round parent and *gg ww* for the green-wrinkled parent.

Diagram of Mendel's Dihybrid Cross

Phenotypes of two parent races	Yellow-round × green-wrinkled			
Their genotypes	*GG*	*WW*	*gg*	*ww*
Their gametes, either male or female	*G*	*W*	*g*	*w*
Consequent genotype of the F_1	*Gg Ww*			
Observed phenotype of the F_1	Yellow-round			
Kinds of gametes produced by F_1 if independent assortment occurs	*GW, Gw, gW, gw*			

All the possible combinations between the four types of male and of female gametes produced by the F_1 are shown in the following "checkerboard" diagram. Each of the 16 squares gives the genotype that would result from one of the possible combinations of gametes and the resulting phenotypic appearance of the plant.

Dihybrid-cross checkerboard		*Female gametes*			
		GW	*Gw*	*gW*	*gw*
Male gametes	*GW*	*GG WW* yellow-round	*GG Ww* yellow-round	*Gg WW* yellow-round	*Gg Ww* yellow-round
	Gw	*GG Ww* yellow-round	*GG ww* yellow-wrinkled	*Gg Ww* yellow-round	*Gg ww* yellow-wrinkled
	gW	*Gg WW* yellow-round	*Gg Ww* yellow-round	*gg WW* green-round	*gg Ww* green-round
	gw	*Gg Ww* yellow-round	*Gg ww* yellow-wrinkled	*gg Ww* green-round	*gg ww* green-wrinkled

We find that Mendel's second assumption—the occurrence of independent assortment—appears to fit and so "explain" his experimental results. If the dihybrid produces four kinds of male gametes in equal numbers and produces the same four kinds of female gametes in equal numbers, and if all possible combinations of male and female gametes take place according to the laws of chance, nine kinds of genotypes will result. We have already seen that in peas, yellow is dominant to green, and round is dominant to wrinkled, so that the nine classes of genotypes will produce four kinds of phenotypes as follows:

Genotype *GG WW*	1 in 16	gives phenotype of yellow and round	9
Genotype *GG Ww*	2 in 16	gives phenotype of yellow and round	
Genotype *Gg WW*	2 in 16	gives phenotype of yellow and round	
Genotype *Gg Ww*	4 in 16	gives phenotype of yellow and round	
Genotype *GG ww*	1 in 16	gives phenotype of yellow and wrinkled	3
Genotype *Gg ww*	2 in 16	gives phenotype of yellow and wrinkled	
Genotype *gg WW*	1 in 16	gives phenotype of green and round	3
Genotype *gg Ww*	2 in 16	gives phenotype of green and round	
Genotype *gg ww*	1 in 16	gives phenotype of green and wrinkled. .	1

If we compare this theoretical expectation with the numbers of each phenotypic class of the 556 F_2 peas that were actually obtained, we find that the correspondence is very close:

Phenotypic class	*Expected F_2 ratio*	*Actual F_2 ratio*
Yellow-round	$^9/_{16}$, or 312.5	315
Yellow-wrinkled	$^3/_{16}$, or 104.25	101
Green-round	$^3/_{16}$, or 104.25	108
Green-wrinkled	$^1/_{16}$, or 34.75	32

The principle of independent assortment that Mendel assumed in order to account for the four phenotypic classes of the dihybrid F_2 was clearly substantiated by further breeding experiments and today is often referred to as *Mendel's second law.* It may be stated as follows: When more than one pair of allelomorphic genes are involved in a cross, each pair assorts *independently* of the others.[1]

THE TRIHYBRID CROSS

Mendel's most elaborate experiment was the crossing of homozygous parent stocks that differed in regard to three sets of characters, or three pairs of genes. One stock was characterized by having round seeds, yellow cotyledons, and a colored (gray-brown) seed coat; the other by having wrinkled seeds, green cotyledons, and a colorless (white) seed coat. This cross is given in diagrammatic form on the opposite page. It will be seen that the new trihybrid phenotypic F_2 ratio 27:9:9:9:3:3:3:1 can be accounted for by the principles already encountered—segregation and recombination and independent assortment—but that the independent assortment of three pairs of genes results in the production of eight kinds of gametes and so requires a "checkerboard" with 64 squares. (The "checkerboard" is omitted in the diagram but may easily be constructed in the same manner as that given for the dihybrid.)

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[1] Later, we shall see that under certain conditions, Mendel's second law does not hold and that it needs additional qualifications.

DIAGRAMMATIC DESCRIPTION OF TRIHYBRID CROSS

P_1 phenotypes	yellow-round-colored × green-wrinkled-colorless							
P_1 genotypes	*WW*	*GG*	*CC*	*ww*	*gg*	*cc*		
P_1 gametes	*GWC*			*gwc*				
F_1 genotype	*Gg Ww Cc*							
F_1 phenotype	yellow-round-colored							
F_1 male gametes	*GWC*	*GWc*	*GwC*	*gWC*	*Gwc*	*gWc*	*gwC*	*gwc*
F_1 female gametes	*GWC*	*GWc*	*GwC*	*gWC*	*Gwc*	*gWc*	*gwC*	*gwc*

The F_2 generation will consist then of:

27 *Distinct Genotypes*				8 *Distinct Phenotypes*
1	*GG*	*WW*	*CC*	27 yellow-round-colored
2	*GG*	*WW*	*Cc*	
2	*GG*	*Ww*	*CC*	
2	*Gg*	*WW*	*CC*	
4	*GG*	*Ww*	*Cc*	
4	*Gg*	*WW*	*Cc*	
4	*Gg*	*Ww*	*CC*	
8	*Gg*	*Ww*	*Cc*	
1	*GG*	*WW*	*cc*	9 yellow-round-colorless
2	*GG*	*Ww*	*cc*	
2	*Gg*	*WW*	*cc*	
4	*Gg*	*Ww*	*cc*	
1	*GG*	*ww*	*CC*	9 yellow-wrinkled-colored
2	*GG*	*ww*	*Cc*	
2	*Gg*	*ww*	*CC*	
4	*Gg*	*ww*	*Cc*	
1	*gg*	*WW*	*CC*	9 green-round-colored
2	*gg*	*WW*	*Cc*	
2	*gg*	*Ww*	*CC*	
4	*gg*	*Ww*	*Cc*	
1	*GG*	*ww*	*cc*	3 yellow-wrinkled-colorless
2	*Gg*	*ww*	*cc*	
1	*gg*	*WW*	*cc*	3 green-round-colorless
2	*gg*	*Ww*	*cc*	
1	*gg*	*ww*	*CC*	3 green-wrinkled-colored
2	*gg*	*ww*	*Cc*	
1	*gg*	*ww*	*cc*	1 green-wrinkled-colorless

CHAPTER XX

The Physical Basis of Inheritance

When Mendel announced the results of his experiments in 1866, nearly all biologists were engaged in the discussions and controversies that followed the publication of Darwin's *Origin of Species* in 1859. The few biologists who knew of Mendel's work did not appreciate its importance, and it was soon forgotten. By 1900, however, many biologists had come to realize that a more precise evaluation of inheritance and variation was essential for the understanding of evolutionary processes, and had turned to experimental studies. In that year, three botanists who were independently investigating inheritance in plants came across Mendel's paper of 1866 and, realizing its value, made it known throughout Europe and America. Almost at once, a number of botanists and zoologists repeated Mendel's experiments, using a wide variety of plants and animals for breeding stocks. Nearly all these experiments verified Mendel's findings and soon established segregation-and-recombination and independent assortment as general principles of biological inheritance.

It must not be supposed, however, that modern genetics consists merely in verifying Mendel's laws and discovering that they apply to organisms in general. Mendel established two basic principles of inheritance and contributed an extremely useful experimental method; but an ever-increasing number of workers and the combination of experimental breeding with other methods of research have carried modern genetics far beyond the point reached by Mendel.

In the interval between 1866 and 1900, tremendous advances had been made in another field of biology that was eventually to become closely knit with Mendelian breeding in the development of modern genetics. This is the science of cell study, or *cytology*. In 1866, the "cell doctrine" was in process of becoming established, but little was actually known about the detailed structure or the lineage of cells, and comparatively few biologists thought in terms of cells. Between 1866 and 1900, however, special techniques for fixing and staining cells to permit microscopic differentiation of their component parts, the invention of the microtome for cutting microscopically thin slices of tissues, and constantly increasing interest in cytological studies led to the recognition of a number of fundamental and universal cell phenomena, particularly *mitosis*, *maturation* (*meiosis*), and the details of fertilization.

The Sutton-Boveri Hypothesis. In about 1902, the American cytologist W. S. Sutton, who was investigating the details of maturation and, like nearly all other workers in biology, had become greatly interested in the newly discovered "Mendelian heredity," saw that there was a striking parallel between Mendel's laws and certain details of maturation and fertilization. He realized that if we but conceive of the Mendelian factors or genes as being located in the chromosomes, then the latter provide a vehicle and a precise mechanism that will account for:

1. *Segregation* of the factors at gamete formation (gametic purity).
2. *Recombination* of the factors at fertilization (zygote formation).

And, if we can assume that the chromosomes at synapsis may have the paternal and maternal elements of each paired set turned at random toward either reduction-division pole, then maturation will also provide a perfect mechanism to account for:

3. *The independent assortment of as many pairs of factors as there are pairs of chromosomes*, so long as each pair of allelomorphic factors is in a separate pair of chromosomes.

Sutton's reasoning was based upon the striking parallels between the phenomena of Mendelian inheritance and those shown by the chromosomes at meiosis. Another parallel cited by Sutton and his followers was also known at this time. We have seen that it makes no difference which parent is tall or which is dwarf; in either case, the F_1 will be tall, and the F_2 will show a ratio of 3 talls and 1 dwarf. We also know that the only thing that the male and female parent contribute equally to the zygote is their chromosome complex. All or nearly all the cytoplasm comes from the female parent, yet the male parent appears to contribute equally with the female to the hereditary qualities of the offspring.

Sutton's hypothesis, which came to be known as the *Sutton-Boveri hypothesis* (after Sutton and Theodore Boveri, the latter a cytologist who contributed much to our knowledge of maturation), at first met with much opposition, but gradually, as more and more evidence accumulated to support it, by 1920 to 1925 it was accepted as a proved principle in biology.

SEX DETERMINATION AND SEX LINKAGE

Shortly after the announcement of the Sutton-Boveri hypothesis, further studies on cytology brought to light still other parallels between chromosomes and certain peculiar modes of inheritance that did not precisely correspond to the original Mendelian types. Soon after chromosomes became well known, it had been found that the cells of each species or kind of organism have a definite and unchanging number of chromosomes. In man, for example, every cell (except matured germ cells) has 48 chromosomes (24 pairs); in the fruit fly Drosophila, every cell has 8 (4 pairs); and in the garden pea, every cell has 14 chromosomes (7 pairs). But now certain exceptions were discovered. It was found that in some species of bugs (Hemiptera), the cells of the females have an even number of chromosomes and those of the male have an odd number, 1 less than in the female. Further study showed that all the eggs of such a species contain the same number of chromosomes (half the female number) but that the spermatozoa are of two kinds as regards chromosome number: half of the spermatozoa have the same number found in the egg; the other half of the spermatozoa have 1 chromosome less. For example, in one species of bug, the females have 12 chromosomes in each body cell, and all the mature unfertilized eggs have 6 chromosomes; but the body cells of the male contain only 11 chromosomes, and half of the mature sperm have 6 chromosomes and half only 5. It seems fairly evident from this that an egg (always with 6 chromosomes) fertilized by a sperm with 6 chromosomes will produce a 12-chromosome zygote and develop into a female, whereas an egg that is fertilized by a 5-chromosome sperm will produce an 11-chromosome zygote and develop into a male.

Later work brought to light other types of "sex determination." In Drosophila and in man, the number of chromosomes is the same in the two sexes, but in both these species one pair of chromosomes, the so-called "sex chromosomes," are alike (XX) in the female and unlike (XY) in the male. As a consequence, when the human egg is formed, it will always contain 23 ordinary chromosomes (*autosomes*) and 1 X chromosome, whereas the sperm are of two sorts—*female-producing* spermatozoa with 23 autosomes and an X chromosome, and *male-producing* spermatozoa with 23 autosomes and a Y chromosome. In poultry and in many of the Lepidoptera (moths and butterflies), a type of sex determination exists that appears to be just the reverse of that in man and Drosophila. Here the male has two X chromosomes (XX); and the female, an X and a Y. Accordingly, all sperm are alike, containing one set of autosomes and an X chromosome, and the female produces two kinds of eggs—one with a set of autosomes and an X chromosome, the other with a set of autosomes and a Y chromosome.

The various types of correlation between sex and chromosomes that are well known in animals may be tabulated as follows (here AA denotes a diploid set of autosomes; A, a haploid set):

Type of sex determination	*Chromosomes of female*	*Kinds of eggs*	*Chromosomes of male*	*Kinds of sperm*
Bug type	AA + XX	(1) A + X	AA + XO	(2) A + X A + O
Drosophila type	AA + XX	(1) A + X	AA + XY	(2) A + X A + Y
Poultry type	AA + XY	(2) A + X A + Y	AA + XX	(1) A + X
Honeybee type.	AA + XX (32)	(1) A + X (16)	A + X (16)	(1) A + X (16) (no reduction division)
	Fertilized eggs develop into females, unfertilized eggs into males			

As soon as the correlation between sex and chromosomes was discovered, it was seen that such a mode of sex determination gave further

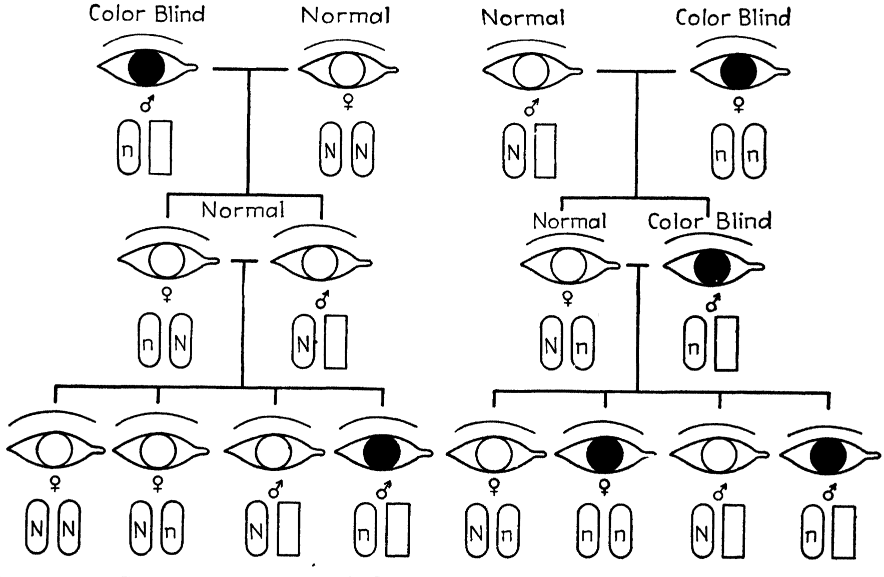

FIG. 104. *Diagram of the sex-linked inheritance of color-blindness in man. N represents the dominant gene for normal vision, n the recessive gene for color-blindness. Note that only the X chromosomes, represented in oval outline, carry N or n. The Y chromosomes are represented by empty rectangles.*

evidence of the residence of the genes within the chromosomes. Long before Mendel's experiments were rediscovered, a peculiar type of inheritance had been noted in man, in which certain recessive traits were most frequently transmitted to the sons but not to the daughters by a normal-appearing mother. *Color blindness*, the inability to distinguish red from green, is such a character; one type of *night blindness*, the inability to see in dim light, is another; and certain types of *hemophilia*, a condition in which the blood lacks the ability to clot, is still another. The peculiar mode of inheritance of these characters is clearly accounted for if we suppose that the genes for color blindness, night blindness, and hemophilia and their dominant allelomorphs are located in the X chromosome. This is shown by the accompanying diagram (Fig. 104), illustrating the inheritance of color blindness, in which the X chromosomes are represented as oval, the Y chromosomes as oblong, N is the gene for normal, and n the gene for color blindness.

Similar cases of sex-linked inheritance are well known in Drosophila. In poultry and in Lepidoptera, the characters found to be sex-linked show an inheritance in exact keeping with the fact that in these groups the male has two X chromosomes and the female but one.

LIMITATIONS TO MENDEL'S SECOND LAW

Until 1906, all the rapidly accumulating crosses that involved two or more pairs of allelomorphs showed the independent assortment postulated by Mendel's second law. Some of the adherents of the Sutton-Boveri hypothesis had speculated that two or more genes might reside within a single chromosome and had pointed out (on the basis of what was then known of maturation—and from what we have seen so far) that such genes would remain permanently associated and invariably be inherited together; but this idea was based upon theoretical considerations, not upon any actually known instances.

And then, in 1906, Bateson and Punnett, in England, encountered a supposedly dihybrid cross in which neither independent assortment nor the permanent association of two genes would explain the F_2 progeny. They crossed a sweet pea that was homozygous for purple flowers and long pollen grains with one that was homozygous for red flowers and round pollen grains. The F_1 had purple flowers and long pollen grains, showing that purple was dominant to red and that long was dominant to round. The F_2 generation, however, showed a marked deviation from that expected on the basis of independent assortment. The actual and the expected (on the basis of independent assortment) ratios of the 6,952 F_2 individuals that were obtained are tabulated below:

Combinations.	Purple-long	Purple-round	Red-long	Red-round
Expected by independent assortment.	$\frac{9}{16}$ 3,910.5	$\frac{3}{16}$ 1,303.5	$\frac{3}{16}$ 1,303.5	$\frac{1}{16}$ 434.5
Actually obtained.	4,831	390	393	1,338

It is evident that there are far too many individuals like the original parents and not nearly enough of the two new combinations. There are, however, 783 (390 + 393) individuals that do show the new combinations, and they rule out the possibility that purple and long and red and round are invariably associated with one another.[1]

A sweet pea that was homozygous for purple flowers and round pollen grains was then crossed with one that was homozygous for red flowers and long pollen grains. (Note that this second cross starts with the other possible combination of flower color and pollen-grain shape.) Again, as would now be expected, the F_1 had purple flowers and long pollen grains, but once again, when the actual ratios of the F_2 were compared with the expectation for independent assortment, there were too many individuals with the combinations shown by the parents—in this case, red and long, and purple and round—and too few with the new combinations—purple and long, and red and round. The actual and the expected ratios for the 419 F_2 individuals are given below:

Combinations	Purple-long	Purple-round	Red-long	Red-round
Expected by independent assortment.	9/16 235.8	3/16 78.5	3/16 78.5	1/16 26.2
Actually obtained	226	95	97	1

No satisfactory explanation of the F_2 ratios obtained by Bateson and Punnett was found until after 1910. In that year, Morgan and his colleagues at Columbia University began to find a similar lack of independent assortment in a number of crosses in the fruit fly Drosophila. Their method of attack was different from that of Bateson and Punnett in that they resorted to appropriate backcrosses to obtain a more direct test of independent assortment and more readily to permit measurements of the extent to which any kind of assortment might occur. They were also particularly fortunate in selecting Drosophila as their experimental organism.

The Backcross as a Test of Independent Assortment. As we have already seen, the direct effect of independent assortment is that the dihybrid, or polyhybrid F_1 individual produces equal numbers of all the possible sorts of combinations of genes. If we return for a monent to Mendel's original dihybrid, it will be remembered that the F_1 yellow-round pea had the formula *Gg Ww* and that to give a 9:3:3:1 F_2 ratio, it must have produced an equal number of *GW*, *Gw*, *gW*, and *gw* gametes. In terms of percentages, it produced 25 per cent *GW*, 25 per cent *Gw*, 25 per cent *gW*, and 25 per cent *gw*.. Now the simplest and most direct way to test this assumption is to cross the bihydrid F_1 back to its pure recessive parent or to this same pure recessive stock. Since the pure recessive can only have the genes *gg ww*, each of its germ cells must be *gw*, and the backcross progeny will show how many of each kind of gene combination occurred in the F_1 gametes. This backcross is tabulated below:

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[1] In such case, the 6,952 F_2 individuals should have shown a ratio of 5,214 purple-long and 1,738 red-round and no others.

Gametes formed by the *Gg Ww* F_1	25% *GW*	25% *Gw*	25% *gW*	25% *gw*
Gametes formed by the pure recessive. .	*gw*	*gw*	*gw*	*gw*
Back-cross genotypes .	25% *Gg Ww*	25% *Gg ww*	25% *gg Ww*	25% *gg ww*
Resulting phenotypes . .	yellow-round	yellow-wrinkled	green-round	green-wrinkled

Morgan adopted this type of crossing in order to study the assortment that took place between various genes in Drosophila, and the four following backcrosses show the actual results obtained for two of the pairs of allelic genes in that animal. Gray body color (*BB*) is dominant to black body color (*bb*), and long or normal wings (*VV*) are dominant to vestigial wings (*vv*). Note that in the "first cross," diagramed below, a homozygous gray-long individual is crossed with a homozygous black-vestigial individual and that their gray-long F_1 progeny are used for two contrasting backcrosses: a *female* F_1 (*Bb Vv*) is crossed with a pure recessive *male* (*bb vv*), and then a *male* F_1 (*Bb Vv*) is crossed with a pure recessive *female* (*bb vv*). In the "second cross," a homozygous gray-vestigial individual was crossed with a black-long individual, and their (again) gray-long F_1 progeny was used for the same two contrasting (or reciprocal) backcrosses.

FIRST CROSS

The homozygous parents	gray-long ×	black-vestigial
	BB VV	*bb vv*
Gametes formed by parents	*BV*	*bv*
The resulting F_1	gray-long (*Bb Vv*)	

1. Backcross made by crossing *female* F_1 (*Bb Vv*) with *male* recessive (*bb vv*): 41.5 per cent gray-long; 8.5 per cent gray-vestigial; 8.5 per cent black-long; 41.5 per cent black-vestigial.
2. Backcross made by mating *male* F_1 (*Bb Vv*) with *female* recessive (*bb vv*): 50 per cent gray-long; 0 per cent gray-vestigial; 0 per cent black-long; 50 per cent black-vestigial.

SECOND CROSS

The homozygous parents	gray-vestigial ×	black-long
	BB vv	*bb VV*
Gametes formed by parents	*Bv*	*bV*
The resulting F_1	gray-long (*Bb Vv*)	

3. Backcross made by mating *female* F_1 (*Bb Vv*) with *male* recessive (*bb vv*): 8.5 per cent gray-long; 41.5 per cent gray-vestigial; 41.5 per cent black-long; 8.5 per cent black-vestigial.

4. Backcross made by mating *male* F_1 (*Bb Vv*) with *female* recessive (*bb vv*) 0 per cent gray-long; 50 per cent gray-vestigial; 50 per cent black-long; 0 per cent black-vestigial.

These results, including the same percentage values, were found to be duplicated whenever the same crosses were made in these same ways. They thus appear to be regular and predictable (under the conditions given), but how are they to be explained? Note that in both the "first" and "second" crosses, the *female* F_1 must form *four* types of germ cells, since when she is crossed to a pure recessive male, four types of progeny are produced, 83 per cent (41.5 + 41.5) like the combinations shown by her parents and 17 per cent (8.5 + 8.5) of the

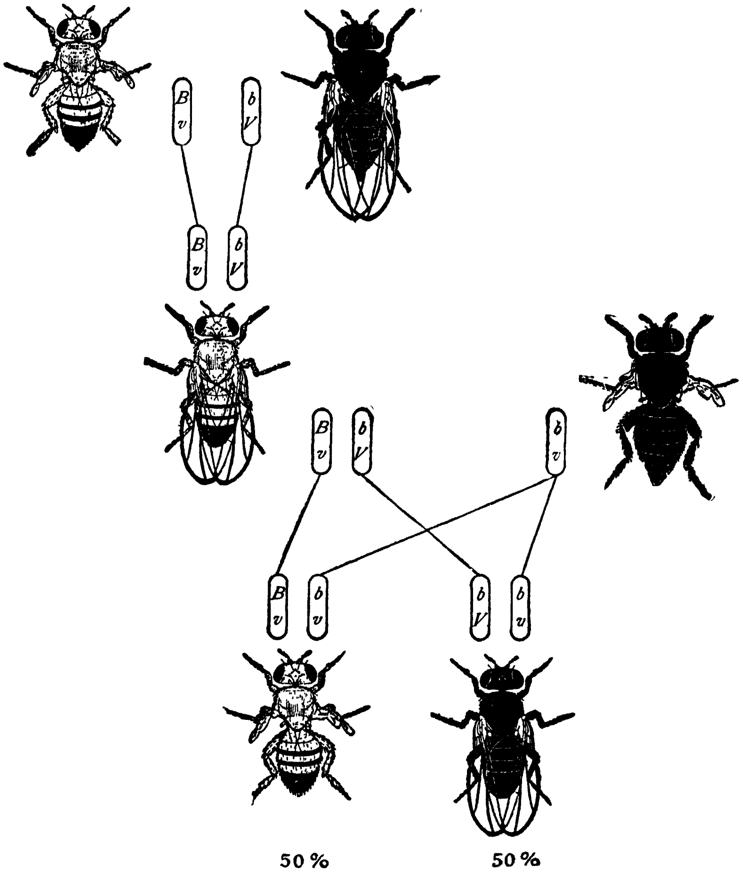

Fig. 105. *The backcross of a male dihybrid, from gray-vestigial × black-long, and a pure recessive black-vestigial female. Note that black and long, and gray and vestigial, show complete linkage. Compare with Fig. 106. (From Sinnott and Dunn, Principles of Genetics.)*

new combinations. When the reciprocal backcrosses are made, however, a *male* F_1 being crossed with a pure recessive female, only *two* kinds

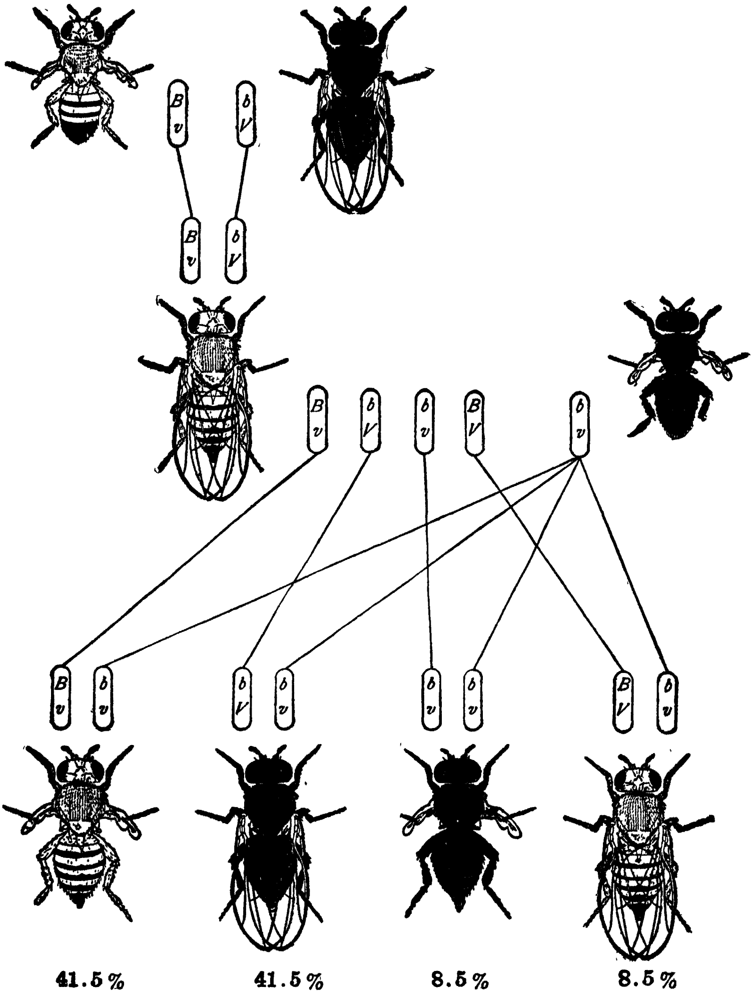

FIG. 106. *The backcross of a female dihybrid, from gray-vestigial × black-long, and a pure recessive black-vestigial male. Note that black and long, and gray and vestigial, are neither completely linked nor do they show independent assortment. Compare with Fig. 105. (From Sinnott and Dunn, Principles of Genetics.)*

of progeny appear, half of them like one of the male's parents, half like the other. Evidently the male forms but two kinds of germ cells.[1]

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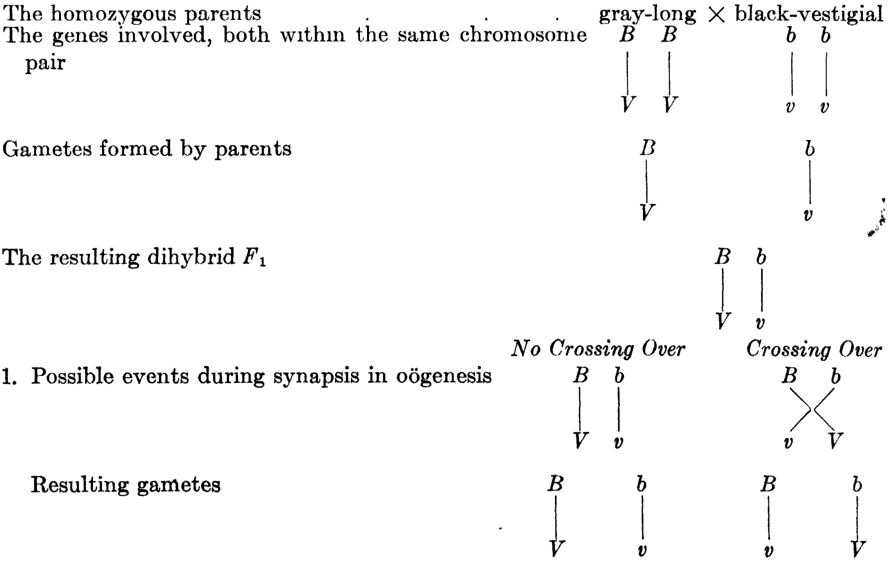
[1] This total lack of any assortment in the male of Drosophila appears to be peculiar to this group and is not characteristic of organisms in general. Such an unexplained difference between spermatogenesis and oögenesis in Drosophila is one but not the

The total lack of assortment in the male could be explained by adopting the Boveri-Sutton hypothesis and supposing that in the first cross, *B* and *V* were in the same chromosome and *b* and *v* were in its mate; and that in the second cross, *B* and *v* were in one chromosome and *b* and *V* in its mate. But how are the 17 per cent of new combinations that are formed by the F_1 dihybrids to be explained?

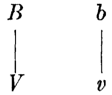
Morgan and his associates were already strong proponents of the Sutton-Boveri hypothesis, and they consequently sought for some explanation that would make the new findings compatible with the evidence that the genes were in the chromosomes. A clue was found in some then recent microscopic studies on the details of early maturation, in which the pairing chromosomes appeared to be twisted about one another at the time they were "fixed" (killed) and stained. Morgan saw in these overlapping chromosomes a possible explanation for his breeding results. If the chromosomes should break at the points where they cross over, and interchange with each other the sections included between the crossings over, it would be possible to see how two or more genes could lie within one chromosome and yet occasionally become separated to form the new combinations that had been observed. Suppose, for instance, that we imagine the conditions and sequences diagramed below, in which the "first cross" in Drosophila is represented with the genes for body color and wing length situated within the same chromosome:


The homozygous parents . . . gray-long × black-vestigial
The genes involved, both within the same chromosome pair
B B V V
b b v v
Gametes formed by parents
B V
b v
The resulting dihybrid F_1
B b V v
No Crossing Over
Crossing Over
1. Possible events during synapsis in oögenesis
B b V v
B b v V
Resulting gametes
B V
b v
B v
b V

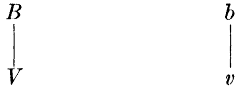
---

chief of the reasons why Drosophila has proved to be such excellent material for genetic studies.

2. No crossing over during synapsis in spermatogenesis



Resulting gametes



Here was a hypothesis that would explain the puzzling, partial, but not completely independent assortment that had been found in one cross in sweet peas and that was now being found in more and more crosses in Drosophila. Such a hypothesis depended upon a number of unproved assumptions about possible happenings in maturation. One marked difficulty was that it depended upon an active process, the twining of chromosomes and the exchanging of genes, which could not be watched under the microscope, since the chromosomes, in order to be seen in detail, had to be fixed and stained, with all processes stopped.

The establishment of this hypothesis involved many technical details that are beyond the scope of our treatment. A new type of genetic research was developed, in which appropriate breeding experiments were checked and compared with detailed microscopic studies of the chromosomes of the breeding stocks. These investigations, which are still actively in progress, have confirmed the supposition that the genes lie within the chromosomes; have demonstrated the processes that provide and account for nonindependent assortment; and have established a number of other principles that appear to be as fundamental as the original "laws" of Mendel. Some of the more important are summarized below:

Linkage. Many groups of two or more genes do tend to be inherited together. Such genes are said to be *linked*, or to constitute a *linkage group*. Four linkage groups have been found in Drosophila, and three of them comprise more than 100 genes each. Linkage groups have also been found in most of the other organisms that have been extensively utilized for breeding experiments—corn (maize), garden peas, sweet peas, rabbits, mice, guinea pigs, and others. The mechanical explanation for linkage is now clearly established to be the fact that all the genes within any one linkage group reside within the same chromosome.

Crossing Over. Linkage was defined as the *tendency* for two or more genes to remain together without segregation. Most linked genes do not show an absolute or invariable linkage. As we saw in Drosophila, if the genes for black and vestigial enter a cross together, they tend to remain associated, but the linkage is occasionally broken (17 per cent of the time, in this instance), and black becomes associated with long and gray with vestigial. Such breakages of a former linkage association, with the consequent formation of a new linkage, is termed *crossing over*, and the new combinations that result are termed *crossovers*. Crossing over was once thought to be rather exceptional, but we now know that the processes that bring it about are a normal event in the very early stages of synapsis of many, probably of all or nearly all, organisms. The essential features of this process and of linkage are shown in Fig. 107.

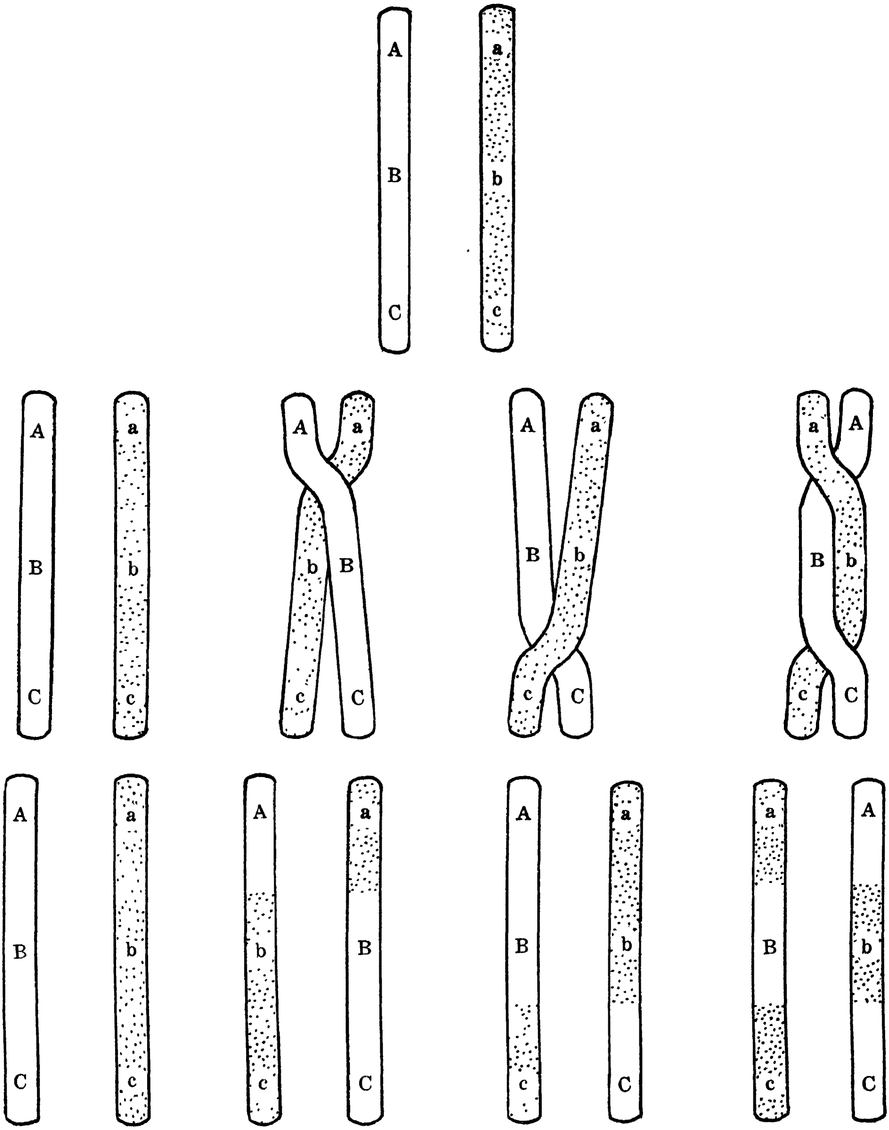

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Fig. 107. *Diagrams illustrating linkage and crossing over.*

Linear Order of the Genes. *All the genes within any one chromosome are arranged in a definite linear order within (or along) that chromosome.* Each gene thus has its own precise location, or *locus,* that will be occupied *only by that definite gene or its allele,* and the characteristic crossover percentages shown by any two linked genes is *a function of the distance apart of their loci.* The loci for black and vestigial, for instance, are 17 crossover units apart, and since the one locus will contain *either* the gene for black *or* the gene for gray and the other will contain *either* the gene for long *or* the gene for vestigial, the crossover percentages between the genes for body color and for wing length will always be 17 per cent, whatever the original combination of the body color and wing length.

CHAPTER XXI

Some Complications of Mendelian Inheritance

Although the more than forty years of ever-increasing experimental studies on heredity since 1900 have abundantly verified Mendel's findings, it would be very misleading to imply that the present-day concept of inheritance is as simple and direct as might be expected from Mendel's original laws. We have already seen that the law of "independent assortment" is limited to special conditions and must be supplemented by the principles of linkage and crossing over when the genes of a di- or polyhybrid are located in the same chromosome. In the present chapter, we shall look at some of the simpler of other complicating conditions that have been discovered by post-Mendelian additions to our knowledge of inheritance.

Absence of Dominance. In all the crosses made by Mendel, the dominance of one allelomorphic gene over the other was a conspicuous feature. Soon after 1900, however, crosses were found in which dominance and recessiveness were not well marked. One of these was in the old-fasioned garden flower, the four-o'clock, in which a red variety crossed with a white variety gives an F_1 that is pale red or pink and an F_2 that consists of $\frac{1}{4}$ red, $\frac{1}{2}$ pink, and $\frac{1}{4}$ white. This F_2 ratio of 1:2:1 is typical of a monohybrid cross when dominance is absent.

A similar case had long been known to poultry breeders, although it was not understood until after 1900. In the Andalusian breed of poultry, there occur black, white, and blue varieties. Of these, the blue was most desired by fanciers, but although the black and white varieties breed true, mating two blues results in $\frac{1}{4}$ blacks, $\frac{1}{2}$ blues, and $\frac{1}{4}$ whites. It is thus evident that blue is due to a heterozygous combination of the gene for black and its allelomorph, the gene for white, and the only way to obtain a brood consisting entirely of blue chickens is to mate a black with a white. Many other crosses that show lack of dominance are known, as well as a large number in which the heterozygote, although much more like one parent than the other, can be easily distinguished from it.

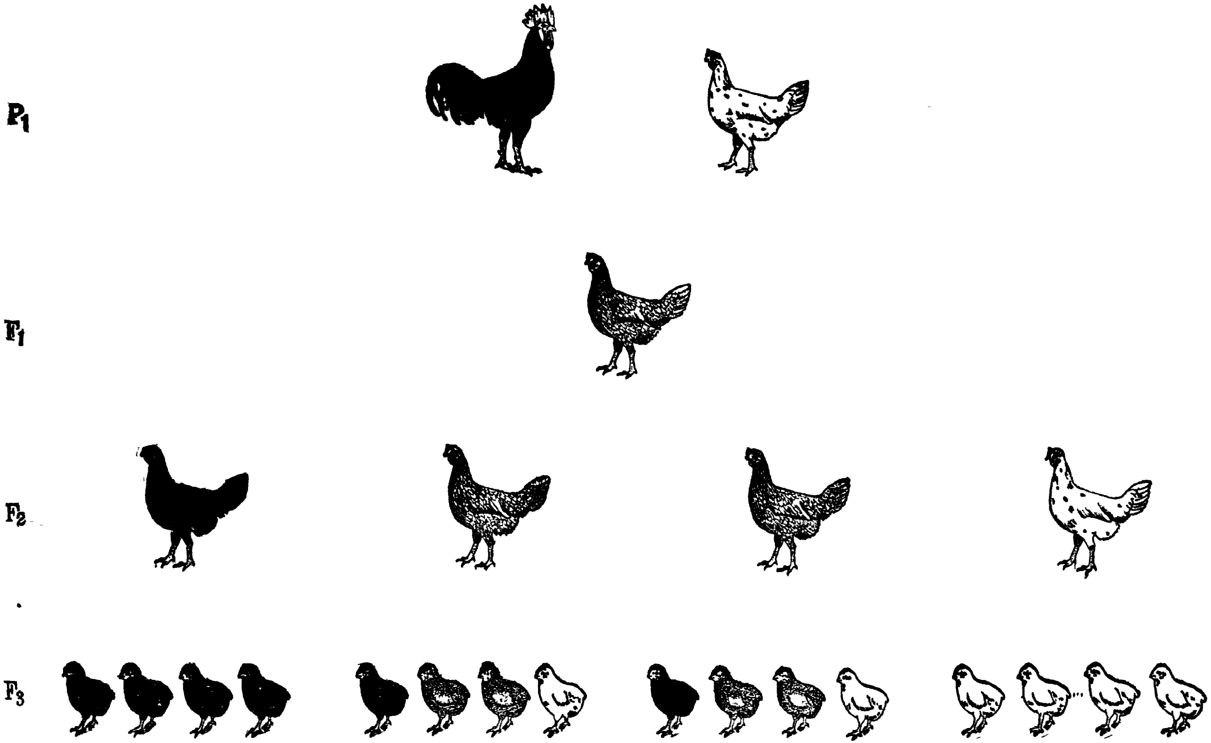

FIG. 108. *The inheritance of blue as the nondominant monohybrid of black and splashed white in the Andalusian fowl.* (*After Sinnott and Dunn, Principles of Genetics*)

Lethal Characters. Among the multitude of genes found to be inherited in various breeding stocks, a number are known that result in the death of the organism *if they are present in a homozygous condition.* The first example of such a gene was found in mice. Repeated experiments showed that when two yellow mice were bred together, the progeny always consisted of 2 yellows to 1 nonyellow, as though 1 individual of a 3:1 or a 1:2:1 ratio were persistently missing. Autopsies on pregnant yellow females that had been bred to yellow males showed that 1 embryo out of 4 always died; and genetic experiments proved this embryo to have been the homozygous *YY* individual. Here, apparently, is a gene that produces yellow coloration as a dominant and some lethal condition as a recessive. Just what this lethal condition may be is unknown, but it is fatal to the developing mouse at a fairly early stage in embryonic existence. Many other lethals are known, some producing death in early stages, some in later stages; but in all cases, such lethals are recessive and show little or no harmful influence when present in a heterozygous state.[1]

Multiple Effects of a Single Gene. It is also now recognized that many genes are not limited to a single effect. We usually contrast (and name) the most striking or immediately evident character that differentiates the phenotypic expression of a dominant gene and its allelomorphic recessive, but closer scrutiny will usually show that several or numerous differences are involved, all attributal to the same pair of genes. For instance, in Drosophila, the genes *WW* and *ww* are spoken of as the genes for red and white eyes, respectively, but the white-eyed recessive also has a colorless testicular sheath and shows a definitely lower vitality than a red-eyed dominant. Many others of the several hundred known recessive genes in Drosophila are correlated with various unnamed structural differences in additional to the more conspicuous phenotpyic effects for which they are named. It is worth noting that in many instances, the several effects attributed to the phenotypic expression of a single gene (or pair of genes) show no evident structural or physiological relationship and give no clue as to why the single gene should produce the particular cluster of effects that is observed.

Genotype and Phenotype. Mendel did not have any reason to differentiate between the visible quality that was inherited and the factor or gene that was transmitted through the gametes and that caused the equality to reappear. Soon after 1900, however, the discovery of other and much more complicated types of inheritance made it extremely helpful to distinguish clearly between the genetic constitution of an organism and its outward appearance. The word *genotype* was coined to refer to a description of the organism in terms of its hereditary-factor[1] make-up, and the word *phenotype* to refer to the outward visible expression of these factors. We have already seen that the phenotype of round and yellow seeds in the pea may be due to a variety of different genotypes—*GG WW, GG Ww, Gg WW,* or *Gg Ww*—and that only breeding tests can distinguish among them. It is well to keep in mind that a gene cannot be seen or directly demonstrated, and in all actual genetic experiments the genotype must be *assumed* from data concerning the appearance and proportion of various phenotypes in certain sequences of generations.

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[1] Compare with the sex-linked condition in man known as *hemophilia.*

THE INTERACTION OF GENES

So far we have been concerned with what have been termed *unit characters.* Here each gene or pair of genes appears to produce a distinct and evident phenotype, and, conversely, each phenotype appears to be due to one gene or one pair of genes. Soon after 1900, however, numerous cases began to be found in which a given phenotype was dependent upon the coincidence of two or more nonallelomorphic genes in the same organism. Today many hundreds of such nonunit characters are known, and they form such a common and important type of genetic phenomena that we shall need to examine a number of representative examples.

Walnut Comb in Fowls. The various breeds of the domestic chicken show a variety of comb forms. Among these are *rose comb, pea comb, walnut comb,* and *single comb.* Breeding experiments show that when a homozygous rose-comb fowl is mated with a homozygous single-comb fowl, the F_1 are all rose comb and the F_2 show a ratio of 3 rose comb to 1 single comb, a typical monohybrid cross. The cross between pea comb and single comb also forms a typical monohybrid cross, with an F_1 all pea comb and an F_2 with 3 pea comb to 1 single comb. When, however,

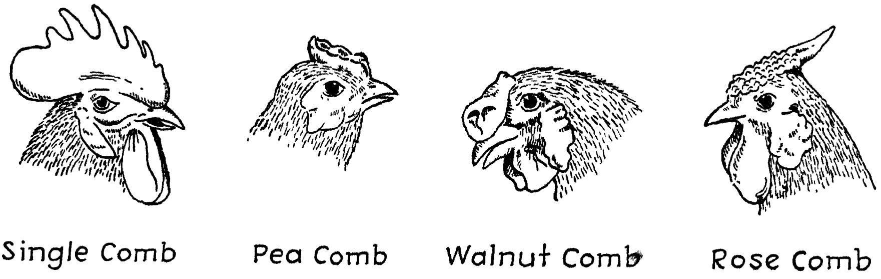

FIG. 109. *Some comb shapes in the domestic fowl.*

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[1] The word *gene* was then coined to refer to a unit of the genotype.

a homozygous rose-comb fowl is mated with a homozygous pea-comb fowl, the F_1 are all walnut comb, and the F_2 gives 9 walnut comb, 3 rose comb, 3 pea comb, and 1 single comb. Walnut comb is thus not a unit character but the phenotypic expression of the genes for rose and pea acting together. Here, if A is used to represent the gene for rose comb and a, its recessive allelomorph, and B is used to represent the gene for pea comb and b, its recessive allelomorph, we may diagram the cross as follows:

Parent varieties	rose comb $AA\ bb$	×	pea comb $aa\ BB$
F_1		$Aa\ Bb$ walnut comb	
F_2	9 ($AA\ BB$, $AA\ Bb$, $Aa\ BB$, or $Aa\ Bb$)		walnut
	3 ($AA\ bb$ or $Aa\ bb$)		rose
	3 ($aa\ BB$ or $aa\ Bb$)		pea
	1 ($aa\ bb$)		single

Complementary Genes. Among the many types of sweet peas, there are two white varieties (the Emily Henderson and the Blanche Burpee) that differ from one another in several structural characters. When these two varieties are crossed, all the F_1 progeny have colored (purplish red) flowers, and when the F_1 are allowed to self-fertilize, the F_2 shows a phenotypic ratio of 9 colored to 7 white flowers. Further breeding has shown that this is really a ratio of $\frac{9}{16}:\frac{3}{16}:\frac{3}{16}:\frac{1}{16}$, in which the last three groups cannot be distinguished phenotypically, and that the genes concerned are C (dominant to c), the gene for chromogen, a colorless color base; and E (dominant to e), the gene for an enzyme that is capable of changing chromogen into a purplish red color.

This may be diagramed as follows:

Parent varieties		white $CC\ ee$	×	white $cc\ EE$
F_1			$Cc\ Ee$ colored	
F_2	9	9 colored ($CC\ EE$, $CC\ Ee$, $Cc\ EE$, or $Cc\ Ee$)—chromogen, enzyme		
	7	3 white ($CC\ ee$, or $Cc\ ee$)—chromogen, no enzyme 3 white ($cc\ EE$, or $cc\ Ee$)—enzyme, no chromogen 1 white ($cc\ ee$)—neither enzyme nor chromogen		

Here we have two sets of genes, neither able to produce a visible effect alone but together producing a visible effect. Numerous other examples of such complementary genes are known.

Modifying Genes. A very common type of gene interaction is that associated with genes which do not themselves produce any visible effect but which have the faculty of modifying the phenotypic expression of some other nonallelomorphic gene. Genes of this sort are very common in the inheritance of the various coat colors of mammals. Among the numerous domesticated varieties that have been developed from the common mouse are a pure white (albino) and a pure black variety. The "wild-type" mouse from which both of these were derived has a characteristic gray color known as *agouti*,[1] a peculiar pepper-and-salt color that is produced by each hair being banded with at least two colors, one basal and one apical.

If a black mouse is crossed with a certain type of albino, the F_1 are all agouti, and these, when mated among themselves, produce an F_2 that consists of approximately 9 agouti, 3 black, and 4 white mice. Here the gene involved are B (dominant to b), a gene for black hair pigment; and A (dominant to a), a gene that causes the pigment in the hair to become localized and not evenly distributed throughout the hair. When no pigment is present, the gene A can have no phenotypic expression.

Parent varieties .		black × white $aa\ BB$ $AA\ bb$
F_1 . . .		$Aa\ Bb$ agouti
F_2 . .	9	9 agouti ($AA\ BB$, $AA\ Bb$, $Aa\ BB$, or $Aa\ Bb$)
	3	3 black ($aa\ BB$, or $aa\ Bb$)
	4	3 white ($AA\ bb$, or $Aa\ bb$) 1 white ($aa\ bb$) a new genotype for white

Other Types of Gene Interaction. Another way in which genes are known to interact to produce a modified F_2 phenotypic ratio is shown by genes that, without producing any visible effect themselves, inhibit the phenotypic expression of another gene. An example is found in poultry, where a gene A (dominant to a) for colored plumage and an inhibiting gene B (dominant to b), if brought together in a typical hybrid cross, result in a colorless F_1 and an F_2 ratio of 13 colorless (white) and 3 colored individuals.

A dihybrid phenotypic ratio of 15:1 is produced by what are known as duplicate genes. Here A is dominant to a, B is dominant to b, and either A or B alone or A and B together produce exactly the same effect. Consequently $AA\ Bb$, $AA\ BB$, $Aa\ BB$, $Aa\ Bb$, $AA\ bb$, $Aa\ bb$, $aa\ BB$, and $aa\ Bb$ are indistinguishable in their phenotypic expression and only the genotype $aa\ bb$ out of 16 shows a visible difference.

Modified trihybrid and tetrahybrid ratios are also known. Among the former are such modifications of the typical 27:9:9:9:3:3:3:1 ratio as 27:9:28, 63:1 and 27:37. Genotypically, such ratios are precisely of the same sort as those of the typical trihybrid, but various types of gene interaction make several of the groups phenotypically indistinguishable.

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[1] The name of the color is derived from the agouti, a South American rodent in which this type of coloration is particularly striking.

THE MULTIPLE-FACTOR HYPOTHESIS

One of the types of inheritance most difficult to understand is that illustrated by the behavior of skin color in the cross between the white and Negro races. The color of the F_1 mulatto is more or less intermediate between that of the two parent races, but the F_2 generation fails to show any clear-cut pattern of segregation. Instead, there results a widely variable F_2, ranging from very light-yellow individuals to others almost as dark as the Negro grandparent. Similar cases are known in other animals and in plants, and for a long time they were regarded as non-Mendelian. That is, since they did not show a clear-cut segregation and recombination, it was assumed that some other and unknown type of inheritance must be involved.

The clue to an understanding of these crosses came from breeding experiments on the inheritance of seed color in wheat and of ear length in corn, which furnish examples of this so-called "non-Mendelian" or "blended" inheritance. In a cross between a certain variety of red-kerneled wheat and a variety of white-kerneled wheat, the F_1 has pale red kernels, and the F_2 is markedly variable, ranging from very pale red to much darker than the F_1, but with few if any kernels as white or as red as the parent generation.

It was finally seen, both by Nilsson-Ehle, who worked with wheat, and by East, who demonstrated a similar condition in the inheritance of ear length in corn, that such cases were probably Mendelian (involving segregation and recombination of genes) but that the Mendelian pattern was concealed by the large number of genes involved. Suppose that the red color in the wheat is due to three pairs of genes, *AA BB CC*, and each of these genes contributes one-sixth of the total redness, so that *Aa bb cc*, *aa Bb cc*, or *aa bb Cc* will produce a kernel one-sixth as red as an *AA BB CC* individual; thus *AA bb cc*, *Aa Bb cc*, *Aa bb Cc*, etc., will produce a kernel one-third as red, etc. In the original cross, the red variety has the constitution *AA BB CC*, the white variety the constitution *aa bb cc*, and the pale red F_1 individuals have the constitution *Aa Bb Cc*. The gametes of the F_1 will be of eight kinds: *ABC*, *ABc*, *AbC*, *aBC*, *Abc*, *aBc*, *abC*, and *abc*, and if all possible recombinations occur, 27 genotypes will be produced, as shown in the following diagram.

1 *AA BB CC* —1 individual in 64 with 6 genes for red

$$\left.\begin{array}{l} 2\ \ AA\ BB\ Cc \\ 2\ \ AA\ Bb\ CC \\ 2\ \ Aa\ BB\ CC \end{array}\right\}\ \text{6 individuals in 64 with 5 genes for red}$$

4	*AA Bb Cc*	15 individuals in 64 with 4 genes for red
4	*Aa BB Cc*	
4	*Aa Bb CC*	
1	*AA BB cc*	
1	*AA bb CC*	
1	*aa BB CC*	
8	*Aa Bb Cc*	20 individuals in 64 with 3 genes for red
2	*AA Bb cc*	
2	*AA bb Cc*	
2	*aa BB Cc*	
2	*aa Bb CC*	
2	*Aa BB cc*	
2	*Aa bb CC*	
4	*Aa Bb cc*	15 individuals in 64 with 2 genes for red
4	*Aa bb Cc*	
4	*aa Bb Cc*	
1	*AA bb cc*	
1	*aa BB cc*	
1	*aa bb CC*	
2	*Aa bb cc*	6 individuals in 53 with 1 gene for red
2	*aa Bb cc*	
2	*aa bb Cc*	
1	*aa bb cc*	1 individual in 64 with 0 genes for red

Here is a hypothesis that seems consistent with many of the crosses that appear to show a blended inheritance. It explains the rarity of the appearance of either parent type in the F_2, the fact that the F_2 is much more variable than the F_1, and the tendency of most of the F_2 individuals to be more or less intermediate. In some of these crosses, as in color in wheat, the parent type does appear in the F_2 about as frequently as once in 64 individuals, and if it is argued that in other crosses the parent types are much rarer than once in 64 individuals (in some, they are practically or actually never obtained), we can refer to the ratios that would occur if four pairs or five pairs of genes had been involved.

Suppose that four pairs of multiple genes, *AA BB CC DD*, had been involved and that each gene contributed one-eighth of the total effect. There would be 16 kinds of germ cells produced by the F_1, and the F_2 would show:

1 individual out of 256 with 8 genes
8 individuals out of 256 with 7 genes
28 individuals out of 256 with 6 genes
56 individuals out of 256 with 5 genes
70 individuals out of 256 with 4 genes

56 individuals out of 256 with 3 genes
28 individuals out of 256 with 2 genes
8 individuals out of 256 with 1 gene
1 individual out of 256 with 0 genes

If five pairs of multiple genes, *AA BB CC DD EE*, were involved and each gene contributed one-tenth of the total effect, there would be 32 kinds of germ cells produced by the F_1, and the F_2 would show:

1 individual out of 1,024 with 10 genes
10 individuals out of 1,024 with 9 genes
45 individuals out of 1,024 with 8 genes
120 individuals out of 1,024 with 7 genes
210 individuals out of 1,024 with 6 genes
252 individuals out of 1,024 with 5 genes
210 individuals out of 1,024 with 4 genes
120 individuals out of 1,024 with 3 genes
45 individuals out of 1,024 with 2 genes
10 individuals out of 1,024 with 1 gene
1 individual out of 1,024 with 0 genes

The necessity of obtaining such large numbers[1] of F_2 individuals, together with the difficulty of separating and classifying all the various phenotypic classes, makes this type of inheritance difficult to study and has necessitated a special statistical or biometrical technique. By such methods, the multiple-factor hypothesis has been abundantly verified, although many cases are far less simple than the ones outlined above. The chief importance of multiple-factor inheritance lies in the fact that a great many of the qualities desired by the practical breeder are inherited in this fashion. Among these are milk production in cattle, egg production in fowls, racing ability in horses, leaf shape in tobacco, and many types of disease resistance in crop plants. There is also much inferential evidence that many important human qualities are inherited in this way.

Breeding experiments are, of course, out of the question in human crosses, but from detailed observational data, Davenport concluded that it was probable that skin color in the Negro-white cross involves four pairs of genes but that the genes in two of the pairs have a much greater effect than do the genes of the other two pairs.

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[1] In actual breeding experiments, the number of F_2 individuals obtained should be at least 10 times or, better, 25 times as large as the minimum number theoretically required to allow each genotype to show.

CHAPTER XXII

Variation as the Basis for Hereditary Distinctions

VARIATION is a common phenomenon among all kinds of organisms and includes many kinds and degrees of difference. Variations in size, in number of parts, in form, in color, and in physiological functions may be either large or small; they may be abrupt and discontinuous or (within large populations) may form minutely graded series. The difference in height between the tall and the dwarf peas of Mendel's experiment, for instance, was both great and abrupt, but we know that differences in height among men may be either large or small and that, if we compare the heights of 1,000 men selected at random, we find an almost perfectly graded series between the tallest and shortest individuals of the whole group.

Practically all the attempts that were made to classify variations before 1900 were based upon some scheme of distinguishing between the degrees, or visible kinds, of differences among individuals. None of these schemes was very satisfactory, because no clear-cut distinction could be made between the proposed classes of variation. With the introduction of experimental breeding, however, it soon became evident that some variations are inherited and that others are not, but appear to be determined by the type of environment in which the organism is placed. This distinction, although often difficult to test, has proved to be a very fruitful one and has made possible a much more adequate knowledge of organic variation.

Environmentally Produced Variations. Once a number of clearly *noninherited variations* were known and could be studied as a group, it was seen that they were all produced by some environmental influence. Literally thousands of experiments and carefully checked observations have shown that both slight and very marked variations may be produced in the form, size, color, functioning, habits, and longevity of organisms by modifying their environment. Changes in temperature, in the kind, duration, or intensity of light, in humidity, nutrition, water supply, amount of exercise, amount of crowding, etc., have all been utilized, singly and in combination, to produce such variations. *But none of these environmentally produced variations is ever inherited beyond the generation in which the soma is directly affected.*

Autogenous Variations. Another large assemblage of variations includes those known to be definitely inherited. Although many of these cannot be distinguished from environmentally produced variations by inspection, experiment shows that they are not due to a response to the environment but must be caused by some internal change in the organism itself. Such internal changes are spontaneous in the sense that they are not produced by any known cause and that they can neither be predicted nor be duplicated by any effort of the experimenter.[1] Such variations first appear in but one or a few[2] of the many individuals that were exposed to the same environmental conditions; but once in existence, the new variation may be passed on to an increasing number of individuals that are descendants of the original variant.

Detailed studies of autogenous variations by the parallel methods of the cytologist and experimental breeder have shown that they are not all of one type. Broadly speaking, they fall into two main groups: (1) variations that are correlated with various kinds of detectable chromosome changes and that show various patterns of inheritance; and (2) variations that behave as units in Mendelian inheritance but that are not accompanied by any detectable change in the chromosomes.

Autogenous Variations Due to Chromosomal Changes. We shall dismiss this group of inherited variations rather summarily, not because they are rare or unimportant, but because at present, at any rate, they are of more interest and importance to the technical geneticist and cytologist than to the general student of biology. It will be well to remember, however, that some autogenous variations are caused by gross changes in the chromosomes—changes that affect several or many genes at once—and that these changes provide valuable material for further studies of heredity and cytological processes. We can characterize the main types of known chromosomal changes associated with autogenous variations as follows:

1. Changes within a single chromosome: losses of a small portion of a chromosome; duplication of a portion of a chromosome; rearrangement

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[1] The fact that exposure of organisms to X rays, radium, and other agents does very definitely increase the percentage of new inherited variations is not a real contradiction of this statement. Such agents do speed up the "mutation rate," but the variations that appear are still unpredictable, are quite like those that appear at a slower rate in the absence of radiation, and they have no discernible adaptation or relation to the agent that increased their frequency.

[2] The finding of a new variation in several individuals simply means that the variation was not *detected* until it had been inherited by the progeny of the original variant.

of parts of a chromosome, so that the normal linear sequence of a given block of genes is inverted.

2. Exchanges of parts between different (nonhomologous) chromosomes, with the result that the original linkage relationships and the meiotic behavior of the chromosomes is modified.

3. Losses or gains of whole chromosomes ("heteroploidy").

4. Gains of whole sets of chromosomes, or the loss of a single set, so that haploid, triploid, tetraploid, or higher polyploid individuals are produced by normal diploid parents.

Autogenous Variations Due to Changes in Single Genes. We have seen that Mendelian inheritance is concerned with the transmission, from generation to generation, of differences in the genotypic constitutions of the original parent stocks. We have also seen something of the evidence that the genotypic constitution is made up of separable and combinable units—genes that occupy definite points within particular chromosomes. So far we have utilized gene differences that were found "ready made" in various Mendelian stocks without question as to their origin. It is now time to see the evidence that the same sort of variations are continuously coming into existence in many (probably in all) races of organisms and that, by inference, all the allelic qualities available to the Mendelian breeder have arisen in the same way in the past.

The most critical and rigorous evidence that a given inherited quality is actually new and was derived by some spontaneous change in the genotype of one of its recent ancestors is provided by stocks of experimental organisms that have been bred for many generations under laboratory observation. These stocks have a long history of continued *inbreeding*[1] that has eliminated any chance that an unknown ancestor might have introduced some hidden recessive into the germ plasm or that the appearance of a new character might have been caused by a new combination of genes already present. When the laboratory stock of the fruit fly *Drosophila melanogaster* was started, the "wild" parents were red-eyed. This normal red-eyed character persisted through many inbred generations, and then a white-eyed individual suddenly appeared in this purebred red-eyed stock. The new variant, a male, was bred to a red-eyed female, and the white-eyed condition reappeared in the inbred descendants of their offspring. White-eyed males and females were then bred together to establish a homozygous white-eyed strain of fruit flies. White-eyed proved to be a sex-linked recessive to red-eyed.

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[1] Inbreeding is the mating of close relatives and results in progeny that have fewer than the theoretical maximum of individuals for recent ancestors. The mating of cousins, for example, reduces the total number of separate great-grandparents from eight to six, and the mating of brother and sister reduces the number of grandparents from four to two. The intensity of inbreeding varies from self-fertilization to cousin mating, with numerous intermediate degrees, but all tend to disclose any recessive genes that may exist in the stock.

During the nearly 40 years that *Drosophila* has been bred in the laboratory, hundreds of pedigreed generations and millions of individuals have been carefully scrutinized by the geneticist. Among this huge number of individuals, more than 500 new variants have appeared, each new character proving to be an allele of some formerly homozygous character of the inbred stock. Similar though less numerous instances of the sudden appearance of new inherited characters have occurred in nearly all the stocks of organisms that have been intensively studied by the experimental breeder—numerous strains of mice, rabbits, poultry, insects, and plants. The field naturalist and the practical animal and plant breeder have likewise encountered hundreds of new variations that, though less critically known, seem undoubtedly to be instances of the same phenomenon.

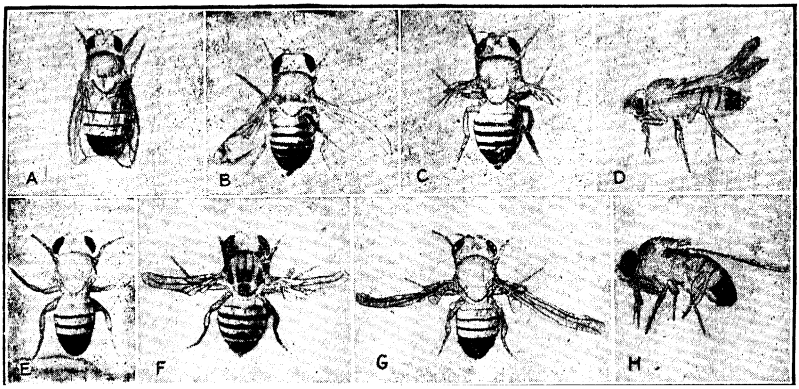

FIG. 110. *Some of the variations, chiefly affecting the wings, which have arisen by mutation in Drosophila.* (*A*) *Truncate;* (*B*) *balloon;* (*C*) *vestigial;* (*D*) *jaunty;* (*E*) *apterous;* (*F*) *strap;* (*G*) *antlered;* (*H*) *dachs.* (*From Sinnott and Dunn, Principles of Genetics*)

The term *mutation* is applied and often restricted to the appearance of a new variation that is due to the origin of a new gene.[1] There is abundant evidence that each mutation is the result of a sudden change in some previously existing gene and that only a single individual gene is concerned. Since the gene that underwent the mutation occupied one definite point (*locus*) in a chromosome, the mutant gene will now occupy that point in all the chromosomes that are derived from the one in which the mutation took place.

We have no definite knowledge of what a gene may be and therefore cannot, of course, know what kind of a change it is that produces a

[1] Originally, the term *mutation* was applied to the appearance of any new inherited character, and it is still occasionally used in that sense, but today it is coming to be restricted to gene or "point" mutations, as distinguished from variations associated with chromosomal changes.

mutation.[1] The great majority of genes are remarkably stable, existing unchanged for hundreds or thousands of generations, and when an occasional individual gene does change, the new mutant appears to have a stability very like that of the original gene from which it came. It is evident that mutations are real occurrences; that they arise spontaneously in the sense that they have no known or predictable cause; and that all of the allelomorphic sets of genes that have been demonstrated by breeding experiments must have arisen through mutation at some time in the history of the race.

Multiple Allelomorphs. So far, we have been concerned with allelomorphic pairs of genes; but a rather large number of cases are known in which three or more different genes show an allelomorphic relationship. Drosophila again furnishes a good example. Some time after the appearance of the mutation "white-eye," another mutation took place in another individual (and in another generation) of homozygous red-eyed flies that resulted in a "peach-" (light yellowish red) eyed individual. The gene for peach proved to be dominant to the gene for white and recessive to the gene for red, and breeding experiments have shown that all these genes occupy the same locus in the X chromosome. All are sex-linked; any given male Drosophila can have only one of these genes, and any given female can have but two. Other sets of multiple allelomorphs are known in Drosophila, and in rabbits, mice, guinea pigs, man (blood types), and a number of plants.

Hybridization and New Combinations of Genes. New inherited variations may also be produced by bringing together new combinations of genes. We have seen that many characters are due to various types of interaction between nonallelomorphic genes, and when certain genes are brought together for the first time, a new character may result without involving any recent mutation. A similar phenomenon is shown in what is known as *reversion.* Not infrequently, when two domesticated races, derived from the same wild stock, are bred together, the progeny (or some of them) show a "throwback" to the ancestral condition, evidently produced by the re-uniting of certain genes that cooperate to produce the original wild type of organism.

HEREDITY AND ENVIRONMENT

We have distinguished among variations that are due to environmental causes and those that owe their existence (and transmission) to genes within the cells. This distinction, although thoroughly justified for analysis and study, gives an incomplete picture of the complexity of the whole problem. Actually any organism is the product of both heredity and environment. We can produce variations either by keeping the heredity uniform and varying the environment or by keeping the environment uniform and varying (by crossing) the heredity, and many phenotypic qualities are demonstrably due to the coincidence of a particular genotype with a particular environment. This is very clearly illustrated by the case of a garden flower, a red Chinese primula. In the primulas, there is a red race that, when crossed with a white race, gives a pink (pale red) F_1 and an F_2 with the ratio ¼ red, ½ pink, and ¼ white—a typical monohybrid in which dominance is lacking. But if the red-flowered plant is taken from the garden and grown in a hothouse at a temperature of 95°F. or more, its flowers will be white. If 10 generations are kept continuously at this high temperature, they will produce nothing but white flowers in all this time, yet if the eleventh generation is returned to the garden, the flowers will again be red. Here the gene that distinguished the red-flowered variety from the white-flowered variety at lower temperatures is *not a gene for red but a gene to produce red at normal temperature and white at temperatures of* 95°*F. and above.*

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[1] There is much inferential evidence that genes are some sort of protein molecules, or groups of such molecules, and that a mutation must be due to some change in the structure and hence in the reactions of the molecule or molecules that constitute the gene.

Many other genes are known that produce one quality in one environment but fail to produce this quality, or produce a different quality, in a different environment. There are also many other characters for which the phenotypic expression of the gene is dependent on the physiological condition (internal secretion) of the organism itself. This is well illustrated in the secondary sexual characters of animals. The natural type and color of a man's beard are inherited (through the mother as well as through the father), but if a man is castrated, he fails to have a beard, and although a woman has factors for a beard—as is shown by her transmitting to her sons the factors for her father's type of beard—she does not develop a beard. The same phenomenon is seen in the inheritance and appearance of horns in certain races of sheep and in the inheritance of the male plumage in birds. A very similar condition is seen in the case of at least certain types of goiter in man, where the development of goiter is dependent upon both genetic factors and the amount of available iodine in the environment.

What Is Inherited? In view of the foregoing considerations and of what we have seen of Mendelian inheritance, we can define inheritance as the transmission from generation to generation of a tendency to react in a certain way to (1) a given environment, (2) a given physiological constitution, and (3) a given complex of other hereditary factors; or, better, since (2) and (3) are also inherited, as the *transmission of a tendency to react in a certain way to a given environment.*

CHAPTER XXIII

Inheritance in Man

DETAILED and accurate knowledge of variation and inheritance in man would probably be of more practical worth than any contribution that biology has made or can make to humanity; but for practical as well as biological reasons, this is probably the most difficult and baffling of all fields of biological research. We have seen that the main key to a knowledge of genetics is experimental breeding—a method which is ruled out in our attempt to understand human genetics. Moreover, both cytological and statistical methods of investigation are most useful and efficient when they can be combined with breeding experiments upon the same stock of organisms, and human cells with their 48 chromosomes are much more difficult to study cytologically than are the cells of Drosophila, with their 8 chromosomes, or the cells of the other organisms from which our knowledge of cytology is mainly derived.

Most of our knowledge of human genetics comes from the scrutiny and statistical study of human pedigrees and from comparison of the modes of inheritance thus indicated with similar pedigrees in experimental organisms. Some special handicaps to this procedure lie in the following conditions: the small size of human families; the very slow reproductive rate, with an average of about 3 or 3½ generations per century; the markedly heterozygous constitution of most human stocks; and the extremely numerous and complicated factors that make up the environment of civilized man.

Heredity Versus Environment in Relation to Man. Perhaps the greatest difficulty of all lies in the fact that any individual man or woman is the product of *both* heredity and environment, and that it is extremely difficult or impossible to know which of his or her individual qualities are chiefly due to heredity and which to environment. We can somewhat clarify the question by an attempt to analyze, define, and distinguish between the two effects.

Sir Francis Galton, who first attempted a careful analysis of the complementary roles played by heredity and environment in man, distinguished between what he termed *nature* and *nurture*. By *nature* is meant all the tendencies, limitations, and qualities that are bequeathed to the individual as maternal and paternal factors at the time of conception. Once a given sperm and egg are fused in fertilization, the full complement of factors is fixed, and the new individual's "nature" is irrevocably determined. From this time on, through the 9 months of embryonic development, through the early years of babyhood and childhood, with their psychological conditioning and training by example, through youth and schooling, many types of environmental influence are shaping the development and phenotypic expression of the particular set of factors that constitutes the individual's "nature." *The sum of all these environmental influences is nurture.*

Since both nature and nurture are absolutely necessary, there is no point in asking which is the more important for the *existence* of the individual. Their real antithesis lies in the different and complementary ways in which they determine the characters of the individual and in which they are or may be manipulated to modify the race. All the evidence from experiment, from checked observations, and from a detailed knowledge of embryonic development strongly supports the conclusion that only the individual's "nature" can be biologically inherited by his offspring. Not any of the influences of nurture, however much they modify, dwarf, or develop the individual, can in any appropriate way modify the factors in his germ cells. This is, of course, a declaration that no characters, qualities, or modifications that are due to the environment or that are acquired by training, practice, or injury can be biologically inherited. The only way an individual's nature can be determined is by controlling what factors shall be brought together when the zygote is formed, and this, of course, can be done only by selecting parents with the requisite genotypes.

It has just been stated that there is "no direct way" in which the environment can influence or change the nature of an individual or of a racial stock. There is, however, an indirect way in which various environmental influences can tremendously affect the genotypic qualities (average "nature") of a race. This is by *selection.* Whenever any environmental influence causes some group of individuals to reproduce more or less than its proportionate share of offspring, then that influence will increase or decrease, for the race as a whole, the proportion of whatever factors are peculiar to or are more concentrated in that group of individuals.

Among the numerous influences that civilization and social organization introduce that indirectly and unconsciously cause selection in human stocks and in national or cultural groups are war, immigration, social and sanitary legislation, and a differential birth rate. We shall look at two of these very briefly. War, insofar as it exposes the strongest and best of a population to increased mortality hazards early in their reproductive period and tends to leave unchecked the reproductive rate of that part of the population that is unfit for military service, provides that proportionately fewer of the better individuals and proportionately more of the poorer will transmit their genes to another generation. (Perhaps one of the clearest and least prejudiced discussions of the very complicated and controversial subject of the biological effects of war is to be found in *War's Aftermath* by D. S. and H. E. Jordan, 1914. This is a study of our own Civil War and its effects on racial stocks.)

NUMBER OF CHILDREN PER 100 WIVES IN SELECTED AREAS OF THE UNITED STATES
(Census of 1910)

Area and classes	*Number of Children*	
	Mothers of all ages at marriage	*Mothers aged 20 to 24 at marriage*
Urban sample		
Professional	151	148
Business.	152	146
Skilled workmen	178	170
Unskilled workmen	213	206
Rural sample		
Farm owners	233	221
Farm renters	258	248
Farm laborers	277	253

RELATION OF SCHOLASTIC RECORD AND ABILITY TO FAMILY SIZE
(Based upon a study of over 3,000 school children in one locality)

Scholastic record	*Number of children per family*	*Rating for ability*	*Number of children per family*
1 (best)	3 30	1 (highest)	3 28
2	3 47	2	4 03
3	3 81	3	4 43
4	4.24	4	5.05
5	4.11	5	5.15

One of the most subtle and persistent types of unconscious selection by society is the *differential birth rate.* The census returns from practically all civilized countries show that the various elements of the population do not reproduce their proportionate quota of offspring. On the contrary, there is almost invariably a definitely *inverse ratio* between the social, economic, and intellectual status of the group and the proportionate number of children it produces. This is illustrated by the tables on page 282, copied from S. J. Holmes, *Human Genetics and Its Social Import,* New York, 1936. An examination of this book will show that these tables are entirely typical of a huge amount of data collected from all nations that provide adequate census material.

The reasons for the differential birth rate are many, but most or all of them arise from the conditions and demands of modern civilization and particularly of urban life. Among the most obvious causes are the later age at marriage of those who are preparing for professional careers or who desire special and prolonged educational advantages; a sense of obligation on the part of more prudent and responsible parents to have no larger families than can be adequately provided with educational, social, and economic advantages; and the fact that large families are felt to interfere with various professional, social, and economic ambitions.

Whatever the cause of the differential birth rate, one thing is evident. A larger proportion of each new generation is produced by parents who have shown the least evidence of ability and a smaller proportion, by those who have shown the most—precisely the opposite of the method man has utilized for the continued improvement of his domesticated races of animals and plants. This leads to one more very important question that we can briefly examine. A question, unfortunately, for which it is extremely difficult to obtain clear-cut *human* data and which is very difficult to free from many types of personal, religious, and social bias.

Are the differences between men, which result in different grades of achievement and ability, dependent upon "nature" or upon "nurture"? Or, to put it another way, can society safely assume that it can maintain or increase the individual and social worth of its members by providing for the maintenance and improvement of nurture alone? If such differences as we see in physical vigor, longevity, temperament, mental ability, and social and individual worth can be explained by the differences in nurture, then selection by war, immigration, or a differential birth rate cannot produce any permanent injury to a racial stock. There is abundant and little questioned evidence that such environmental factors as sanitation, medicine, education, material welfare, and a measure of leisure are of great importance, and that inequalities in sharing these advantages explain many of the differences among men. But the indications that the individual's *capacity* for mental, physical, and moral development is determined by his nature are even more clear-cut and unmistakable. Evidence from many sources indicates that men differ tremendously as to the kinds of genes they receive at fertilization and that this gene complement (nature) at the same time limits and determines the extent to which they can utilize and profit from whatever type of nurture they encounter. There is, indeed, much evidence for the conclusion that the effectiveness of any nurture that society can provide is dependent upon the maintenance of a superior nature for at least a part of the population.

Some of the kinds of evidence for the biological inheritance of human qualities are as follows:

1. *Family pedigree,* in which physical and mental traits can be traced through many related individuals and the mode of inheritance correlated with known types of inheritance in experimental animals. By this method the inheritance of several hundred human characters has been clearly worked out. The difficulty here is that the method works best for simple cases of inheritance—unit characters and the less complex types of modifying and complementary factors—and is difficult to use in cases where there is complex interaction of genes or where environmental influences affect the phenotypic expression of the genes.

2. *Comparisons of the Degrees of Resemblance and Difference between Uniovular (Identical) Twins on the One Hand and Biovular (Fraternal) Twins on the Other.* This is a very good source of data because of the fact that uniovular twins should have identical genotypes; biovular twins should differ in genotypes as much as do ordinary brothers and sisters; and both types of twins should have the same degree of similarity of environment for the two individuals concerned. The evidence from these data very strongly emphasizes that most of an individual's capacities and qualities are determined by his nature, but gives little information as to the particular genes that are concerned or their mode of interaction.

3. *Application of the Results Obtained by the Experimental Breeding of Other Animals to the Interpretation of Human Heredity.* There is positive and unmistakable evidence of the role and importance of the genetic constitution (nature) in all organisms in which experimental breeding and selection are possible. Selection is demonstrably able markedly to increase or decrease the learning ability of rats, the resistance or susceptibility of mice to cancer, and the longevity of Drosophila, and it has been shown in these same animals that, so long as the genotype is unmodified, the environment can produce no permanent change in the stock. When we reflect upon how closely and invariably man's structure and functioning conform to the same laws and principles that apply to other organisms, it seems extremely unlikely that man would show a different relationship in the interaction of his nature and nurture.

The Eugenics Movement. Because of the promise for racial betterment that an application of human genetics would appear to hold out for society, many people have become actively interested in the effort to make such an application on the basis of our present knowledge. This practical program of improving the human stock through an application of the findings of human genetics has been termed *eugenics*—the science of being well born.

Theoretically, there is little reason to question the fact that *if* mankind could be subjected to the same procedures of rigid selection and controlled breeding that have produced our purebred strains of horses, dogs, cattle, and crop plants, he, too, could be molded into a wide variety of pure-breeding strains. Under this procedure, it would be entirely possible to develop a human race that would be homozygous for many desirable qualities and that would at the same time be free from many of the inherited liabilities that now affect many otherwise superior stocks. Actually, of course, this "if" is impossible, and it certainly would be undesirable. The qualities needed in a human society are far more complex and varied than those that are sought for in any of the domestic breeds that man has developed; and the very uniformity so characteristic and desirable in purebred races would probably be very undesirable in human society.

There are, however, many details and tendencies in human inheritance that do appear capable of practical management and control. A rather large number of human qualities or capacities that are known to be inherited can be clearly evaluated as definitely good or bad, no matter what the remainder of an individual's genotype may be. It is largely with such qualities that eugenics is concerned. It seeks to recognize and evaluate an increasing number of these qualities, to determine the precise mode of their inheritance, to discover the various ways in which they may affect the phenotype, and to weigh the practicability of the application of this knowledge by the individual, the family, and the state. Nearly every modern nation has its endowed or state-supported eugenics foundation, devoted to the discovery, dissemination, and ultimate application of the facts and principles of human genetics. Thus far, the practical possibilities of eugenics have hardly been evaluated, but within the last half dozen years, new methods and statistical techniques have made possible a much more rapid accumulation of accurate knowledge. Here may be mentioned the increasing attention to human genetics in medicine and the importance that a knowledge of the patient's inherited constitution often has in diagnosing his condition and in indicating an advisable mode of treatment.

To date, much of the attempt actually to apply genetic procedures to race betterment has been of the sort known as *negative eugenics; i.e.,* to limit or check the undue increase of clearly defective stocks. A number of human qualities that are unquestionably highly undesirable in any individual or member of society have been shown to be inherited. Among such characters are certain forms of mental deficiency, various types of mental derangement, and several forms of severe structural or physiological deformities that condemn their possessors to feeble-mindedness, incurable insanity, or completely disabling physical handicaps. The individual who has inherited such defects not only constitutes a noncontributing burden to society (and often to himself) but also carries a germplasm that will reproduce the same kind of unfortunate and unwanted individuals in the next generation or that will contaminate any better germ plasm with which it may be mixed. The fact that such defective individuals are often incapable of the personal or social responsibility that would lead them to refrain from reproduction places the responsibility upon society and the state.

Two possible methods of state control of defective potential parents have been suggested and to some extent practiced. Defective individuals who owe their condition to a defective germ plasm can be segregated from any opportunity for mating, or such individuals can be made permanently sterile by a surgical operation. The expense and difficulty of segregation are so great that it is hardly practical, but modern surgical techniques have perfected a relatively simple and safe operation that produces complete sterility without interference with the normal sex life of the individual. Here, of course, we encounter a number of legal, political, and religious considerations that, whatever their validity from biological point of view, form a part of any practical eugenics program.

Some 27 of our states and at least 2 provinces of Canada have passed eugenic sterilization laws. In most of these, the laws have geen largely or wholly unenforced. In California, however, the sterilization of defectives (almost wholly feeble-minded) is receiving a practical and rather extensive trial (more than 14,000 hereditary defectives having been sterilized by the end of 1938) and appears to be gaining in public approval as a practical measure.

At best, the sterilization of defective stocks can raise the average of a nation's collective germ plasm only by restricting the increase of its poorest part. Positive eugenic measures appear to be much more promising as a long-time program for human betterment. At present, its program is chiefly that of gathering more precise data about human inheritance and of disseminating these facts and their implications throughout society.

PART III

THE CHANGING GENERATIONS

The Evolution of Life in Time and Space

CHAPTER XXIV

How the Concept of Organic Evolution Developed

In the first part of this book, we studied individual animals and plants at close hand, observing the details of their structure and the ways in which they perform the tasks necessary for self-maintenance. In Part II, we stepped back a little, so as to include within our view not only the individual organism but also its immediate ancestors and progeny. There we saw them as links in the chain of inheritance that connects preceding with following generations. Now we are ready once more to change our viewpoint; this time, we climb to a hilltop, so to speak, from which a broad prospect of the world of life may be had. From this point of vantage, we now direct our gaze back along the path that life has followed, tracing the lines of ancestry until they disappear in the mists of the remote geological past. Finally, when in Part IV we shall again turn to survey the contemporary world and observe on every side the complex interplay between organism and organism and between organism and environment, we shall see in these interrelationships not only the expression of individual functioning and genetic variation but also of the past history of life.

In the present section, we are concerned with animals and plants viewed as the products of a germ plasm of vast antiquity—a germ plasm that has been continuously changing with the passage of time. This aspect of life is summed up in the phrase *organic evolution.* Among the problems here to be considered are the explanation of the deep-seated similarities that underlie the diversities among organisms; the question of the origin, nature, and significance of species; the reasons for the peculiarities of the faunas and floras of different regions of the earth; and the nature of the changes that have occurred among living things during bygone eras.

The Variety and Multiplicity of Living Things. One of the most striking phenomena of life is the tremendous number of different kinds of organisms that now exist. Just how many kinds of animals and plants there are we do not know; more than one million species[1] have already been described and named, however, and it is not improbable that as many more remain to be discovered. Within this vast array, we encounter the widest variations in size, form, degree of complexity, methods of self-maintenance and reproduction, and relations to other organisms. The size range extends from the ultramicroscopic to such enormous living things as whales and sequoia trees. At one end of the scale of complexity are the single-celled bacteria, in which not even a nucleus is visible; at the other are animals and plants made up of billions of specialized, highly integrated, cooperating cells. Inside the limitations imposed by the two great nutritional methods—food manufacture in plants and food capture in animals—there are great differences in the arrangements for doing the tasks necessary for individual maintenance, accompanied by striking modifications in body form and organization. As for environment, animals and plants live in almost every conceivable type of terrestrial and aquatic situation. The seas, the streams and lakes, the soil, the forests and grasslands—all are populated by myriads of living creatures. Even the driest deserts, the arctic wastes, the lightless depths of the ocean, and springs of steaming hot water are not without their inhabitants.

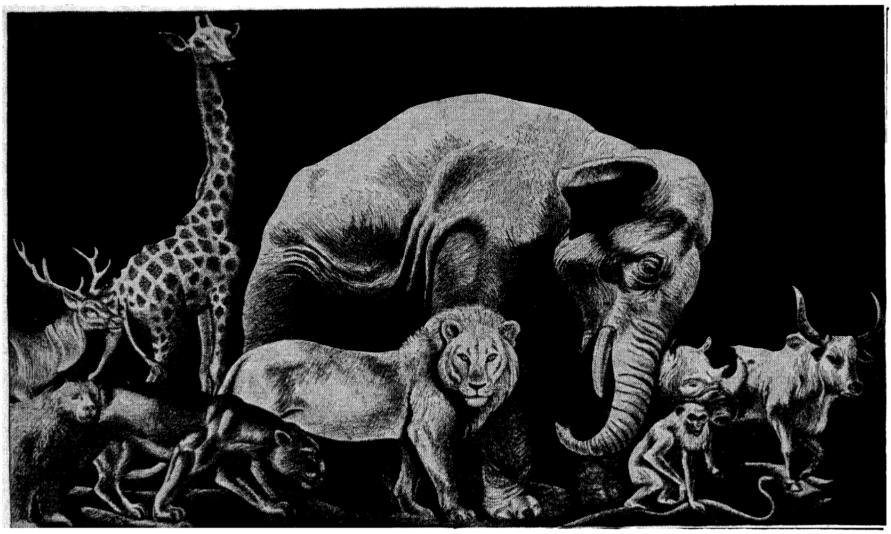

Fig. 111. *"One of the most striking phenomena of life is the tremendous number of different kinds of organisms." (Rearranged from a picture by Artzybasheff, from the jacket of Hegner, Parade of the Animal Kingdom, The Macmillan Company.)*

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[1] According to a careful recent estimate, there are now more than 750,000 described species of animals and more than 600,000 described species of plants.

It is a major concern of the biologist to comprehend the significance of this multiplicity and diversity of living things. How did all these kinds of animals and plants come into existence? What is the meaning of the orderliness that underlies their variety of form and structure? How does it happen that each species has its own particular type of living place and that it occurs only on some definite part of the earth's surface and not elsewhere? And why is it that, although most organisms seem to be well adapted to their environments, they are rarely perfectly so?

The answers to these problems are sought by work along many lines. The biologist studies the life of the past by means of the fossils buried in the layered rocks; he seeks thus to learn of the changes that have occurred in particular groups of organisms through long periods of time and to determine how far back into the past he can trace the ancestry of modern species. He investigates the structure and development of existing kinds of organisms, seeking clues to their relationships through concealed but fundamental similarities among them. He observes the variations that occur among the members of a single species and experiments to determine how these differences are transmitted from generation to generation and what influences determine their preservation or elimination. He studies species as populations occurring in the wild, observing how their individuals differ, on the average, from place to place and from one environment to another, and he attempts to relate these phenomena to present and past isolating factors and to the data from genetic research.

The results and conclusions reached through the combined studies of hundreds of men, scientists of all nationalities, working in all parts of the world over a long period, have been embodied in the great generalization known as the *principle* or *doctrine of organic evolution*, which is to be the theme of this part of our survey of the biological world.

THE DEVELOPMENT OF THE DOCTRINE OF ORGANIC EVOLUTION

Organic evolution is today accepted by practically all scientists as a firmly established principle. It has not long held this status, however, and even now is regarded as a mere unproved theory or rejected altogether by considerable numbers of otherwise well-informed people who are untrained in objective scientific thinking or who lack biological background. The reason this attitude toward organic evolution still survives, whereas other scientific generalizations of corresponding scope are unquestioningly accepted, is the conscious or unconscious assumption that man is something apart from the rest of the universe, differing qualitatively from other organisms—the center and apex of creation, so to speak. To many persons, therefore, anything that shows man to be related, however distantly, to the rest of the animal kingdom is objectionable or even sacrilegious, if the Mosaic account of creation is taken literally. Here the *objectivity* of science has often come squarely into conflict with popular belief and emotion, producing bitter controversies over evolution—now, fortunately, almost a thing of the past. The historic background of this conflict and the nature of the evidence that *forced* students of science to accept the reality of organic evolution, will first be traced in brief review. Here we shall once again see the scientific method at work—the somewhat groping formulation of hypotheses to explain and correlate a mass of observations that men felt must have some meaning; the testing and revision of these hypotheses, some being discarded as false, one becoming eventually established in modified form as one of the principles of science. In later chapters, we shall review the nature of the evidence that led to this result.

Early Evolutionary Speculation. From the earliest times, men have sought a satisfying explanation of the universe and of their own place and significance in the scheme of things. Prior to the development of science, it was natural that their explanations generally took the form of nature myths, in which plants, animals, and men were created by some supernatural agency. Such creation myths have arisen among nearly all primitive peoples. However, evolution has left so many clues and traces that we can scarcely suppose that they passed altogether unnoticed; it is probable that an occasional exceptionally acute observer and profound thinker must have caught glimpses of the truth even before the dawn of history.

However this may be, the oldest records of evolutionary speculations that have come down to us are the ideas of certain Greek philosophers of the sixth and fifth centuries B.C. These men had little biological knowledge to guide them and were groping in the dark; it is natural that their ideas should have been extremely vague, and, although they are interesting, they are not really anticipatory of modern evolutionary doctrine as is sometimes claimed. During this early period of Greek philosophy, a materialistic attitude prevailed, and purely natural causes were sought for all phenomena—a viewpoint not far removed from that of modern science. Later, under the influence of Socrates and Plato, a reaction from this attitude took place. Material phenomena came to be regarded as the mere outward expression of abstract ideas, which were the true realities. Aristotle (350 B.C.), the greatest of the Greek natural philosophers, was the prime exponent of this view. Scientist as well as philosopher, Aristotle knew more about animals and plants than any man of his time or for generations to follow. He wrote a detailed treatise on the animals known to him, including many accurate observations on their anatomical structure. Through his wide acquaintance with organisms and his use of the comparative method of study, he was aware of the fact that they form graded series from lower to higher types of organization, and he drew from this the correct inference that they have evolved. He looked upon their evolution from lower to higher grades, however, as a striving toward the expression of an ideal "archetype" established by a supreme intellect.

The Doctrine of Special Creation. After this early flowering of science in Greece, more than fifteen centuries elapsed before progress in biology was resumed. This long interval saw the rise and fall of Rome, with its essentially utilitarian philosophy, the barbarian conquests, and the confusion of the Middle Ages. During this time, paganism was supplanted by Christianity throughout nearly the whole of Europe, and the church grew immensely in authority. Religion, commerce, and war were dominant in men's thoughts, leaving scant room for science. The crusades during the eleventh to the thirteenth centuries brought the Western peoples into contact with the Arabs, among whom such sciences as mathematics, astronomy, and medicine had been carried to a rather high development. This may have had something to do with the intellectual revival in Europe that, beginning in the eleventh century, culminated in the Renaissance during the fifteenth and sixteenth centuries. Now that men's interest and intellectual curiosity began once more to turn to the world of nature, they were furnished with a ready-made explanation of the origin of living things in the Mosaic account of creation given in the Bible. Not only was this the official and respectable belief but, infused during youthful training, it seemed to make any other explanation of the origin and diversity of life unnecessary.

For more than a millenium, from the Middle Ages until about the middle of the last century, the great majority of people in Christian lands thought that the world had been suddenly created only a few thousand years ago. The church eventually lent its authority to the literal interpretation of the story of creation told in the book of Genesis, according to which all the species of animals and plants were created to populate the newly formed earth, with the making of man as the last and crowning event. It was only about 300 years ago that Archbishop Ussher, a church authority, calculated that creation occurred in the year 4004 B.C., and even determined the day and hour when man was called into being. This date is still to be found as a marginal notation in some editions of the Bible.

The Theory of Catastrophism. From the time of the Renaissance onward, more and more persons became interested in the study of the earth and of the organisms that inhabit it. It had long been known that the rock layers were filled with objects that looked very much like shells, bones, and other parts of animals. Many of these fossils,[1] found far from the sea and even high up on the flanks of mountains, nevertheless had the appearance of creatures that once lived in the sea. Others were altogether strange; some of these were great toothlike or bonelike objects but were unlike the teeth or bones of any known creature.

With the renewal of interest in natural phenomena, a controversy sprang up over the nature of these "fossilia." As early as the fifteenth century, the versatile artist, inventor, and scientist Leonardo da Vinci correctly interpreted them; but such interpretations were so unorthodox that many curious hypotheses were advanced by others to explain in a less disturbing manner the occurrence of fossils. Eventually, however, the conclusion could no longer be resisted that they actually were the remains of animals long dead. As knowledge of comparative anatomy increased, it became possible to assemble and fit together fossil bones to form more or less complete skeletons, from which the appearance of the animals in life could be deduced. Many of the types so reconstructed proved to be unlike anything that now exists, either in Europe or, as exploration gradually showed, anywhere else in the modern world. The early reconstructions of fossils were, to be sure, often faulty and sometimes bizarre, but this served merely to exaggerate an essentially true conclusion—that many animals that formerly existed have since completely disappeared. Today this idea of extinction is so familiar that we can hardly imagine how strange and revolutionary it then seemed.

At about this time, many people realized that the occurrence of extinct types of fossil animals in the rocks need not conflict with but might actually support the Biblical account, if it were assumed that they were the remains of those killed by the Noachian deluge and buried in its sediments. Soon, however, it developed that each great rock formation had types of fossils that did not occur in the layers above and below it; furthermore, there began to be much evidence that the earth had been in existence considerably longer than a few thousand years. Confronted by these difficulties, the adherents of special creation advanced the theory of *catastrophism*—the idea that there had been a succession of great catastrophes, in which all the life of the time was destroyed by flood or fire, followed each time by a new creation of other and higher types. According to this hypothesis, the creation recorded in Genesis was the culmination of a series of such acts and the Noachian deluge, the last of the great catastrophes. Unfortunately for this view, a new interpretation of earth history was shortly to appear and sweep away the assumptions upon which the whole concept was based.

The Establishment of the Uniformitarian Principle. While the leading geologists of the time were still engaged in heated debate concerning the nature of the catastrophes supposed to have overwhelmed the earth at intervals, there occurred an epoch-making event in the history of science. This was the appearance of a paper entitled "Theory of the Earth," presented in 1785 to the Royal Society of Edinburgh by James Hutton. In later years, Hutton expanded and revised this treatise, and it was published as a two-volume work in 1795. It laid the foundation upon which the modern science of geology has been built.

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[1] From the Latin *fossilium*, "something dug up."

Like so many of the great amateurs of science, Hutton had been trained in medicine, though he became a practical agriculturalist. He was much interested in natural history and for many years devoted a great deal of time to the study of meteorology, mineralogy, and geology. His observations gradually led him to a new concept of earth history, in which catastrophism had no place.

Where others had seen in rivers merely streams of water that of course flowed in valleys, since these were the lowest parts of the land, Hutton realized that the rivers themselves had made their valleys by cutting down their beds and by carrying away the weathered rock washed down the valley sides by rain. In place of the accepted idea that the rock strata represented the deposits left by universal floods, Hutton's conclusion was that they were the weathered products of the land, eroded away and carried into former seas by former rivers, to be laid down on the sea floor, just as muds and sands were being deposited in his own time off the mouths of the Scottish estuaries. He saw how the storm waves beat against the shore, undermining the sea cliffs and grinding up the boulders that fell from them into sand and mud that joined the other deposits on the bottom. Nowhere did he find traces of world-wide cataclysms or of the operation of any processes that could not be seen at work today. It was true that the lands showed evidence that sea-laid sediments, consolidated into rock, had been disrupted, upheaved, and injected with veins and masses of molten rock through the agency of subterranean heat; but these effects had been more or less local and were evidently akin to those produced by present-day volcanoes. Furthermore, earth processes appeared to repeat themselves in never-ending cycles; no sooner were new lands uplifted above the sea than atmospheric decay and stream erosion must once more begin to destroy them and make new rock layers from their debris.

Thus Hutton everywhere found evidence of the slow, long-continued, and orderly working of familiar everyday processes, and was forced to conclude that the geological forces that had been at work in the past were largely the same as those now operative. In a well-worn phrase, "study of the present is the key to the past." This thesis, christened *uniformitarianism*, is today accepted with but slight modification as a fundamental principle in geology, at least for all that part of earth history during which life has existed.

Let us pause here to note that the discovery of this principle resulted largely from two qualities of Hutton's work—continued, detailed, and critical observation of natural phenomena, unbiased by preconceptions; and a cautious and sober attitude in attempting to explain the facts thus gathered. It is perhaps significant in this connection that Hutton was Scotch in nationality. He and his followers merely applied in science a rule old in logic but often violated in early geological speculation and even today in ordinary thinking. This is the *rule of minimum hypotheses,*[1] which may be stated as follows: Of all conceivable hypotheses that can be made to explain a given set of facts, those are to be preferred which (1) are most consistent with the data, (2) remove the most difficulties, (3) are simplest, and (4) require the fewest assumptions. The hypothesis (now the principle) of uniformitarianism met these requirements admirably, whereas the hypothesis of catastrophism failed to do so.

Hutton's work at first attracted little attention, partly because the style of his writing was involved and was difficult to follow. The wide influence that it eventually exerted was brought about by two other men, John Playfair and Sir Charles Lyell. In 1802, Playfair published his *Illustrations of the Huttonian Theory of the Earth,* in which the uniformitarian thesis was further explained and developed, and documented with numerous detailed and concrete examples. Lyell, originally a catastrophist, was convinced by the work of Hutton and Playfair. The most famous geologist of his day, he definitely established the principle of uniformitarianism as one of the foundation stones of his science, through the world-wide influence of his treatises and textbooks.

The Length of Geologic Time. Hutton, Playfair, Lyell, and the other men who helped to create the modern science of geology all helped to prepare the way for the establishment of evolution as a fundamental biological principle. So long as earth history could be supposed to have comprised only a few thousands of years, or so long as men could take refuge in the idea that sudden departures from the "order of nature" could be relied upon to explain awkward facts, the mind could still accept a belief in special creation without too much strain. But the establishment of the principle of uniformitarianism changed all this. Since, according to this principle, small and slowly acting forces have worn away the mountains and filled up the seas with their debris, it must follow as a necessary corollary that geologic time has been immensely long. In our own day, we have become inured to the incomprehensibly huge figures used by the modern astronomer and geologist to express space and time, and it is hard for us to realize the shock that it was to an earlier generation, accustomed to thinking in terms of mere hundreds or thousands of years, to find that the world was so immensely old. Hutton himself was awed by the vista that his studies had revealed. In his own words,

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[1] Special application of the logical principle enunciated by Duns Scotus and later emphasized by William of Occam (1347 A.D.), after whom it is called "Occam's razor"· *Entia praeter necessitatem non sunt multiplicanda*—"the number of entities should not be increased unnecessarily."

> When, to a scientific view of the subject, we join the proof which has been given that in all quarters of the globe, in every place upon the surface of the earth, there are the most undoubted marks of the continued progress of those operations which wear away and waste the land, both in its heighth and in its width, its elevations and extensions, and that for a space of duration in which our measures of time are lost, we must sit down contented with this limitation of our retrospect, as well as prospect, and acknowledge that it is in vain to seek for any computation of the time during which the materials of this earth have been prepared in a preceding world, and collected in the bottom of a former sea.

The idea that geologic time has been very long, so revolutionary in those days, has now become a textbook commonplace; and although to Hutton the attempt to measure geologic time seemed vain, men have by now succeeded even in doing this. By combining all that astronomers, physicists, chemists, and geologists have learned about the subject, it has been determined that the earth was born from the sun, probably about 2 billion 500 million years ago, and that as early as 1 billion 800 million years ago it had reached something like its present physical state and may have been capable of supporting life. Actual traces of life have been found in rocks that, by the best methods of estimate, are between 600 and 900 million years old. One need not take these figures too literally; they are chiefly of interest as indicative of the general order of time magnitudes involved. Probably no one would be seriously perturbed if it were found necessary to cut the estimates in half. From the standpoint of the biologist, it would seem of little moment whether life has endured for 1,800 million, 1,000 million, or even a mere 500 million years; any of these times seems amply long to have permitted the occurrence of the changes in life that are recorded in the rocks.

Attempts to Formulate an Evolutionary Hypothesis. Although no satisfactory theory of evolution could be formulated prior to the establishment of the uniformitarian principle and recognition of the great age of the earth, one should not suppose that evolutionary speculation remained at a standstill until after the appearance of Hutton's work. All through the eighteenth century, developments in all branches of science made it increasingly evident that the doctrine of special creation was inadequate. As geological exploration widened, the abrupt breaks between the faunas of contiguous rock formations, supposed to have been caused by catastrophic extinctions followed by new creations, were in many instances found to be bridged over in the rocks of other regions. In numerous groups, the fossils were seen to show a gradual transition from types quite unlike modern ones, in the older rocks, to other types increasingly like those of today in the more recent strata. As exploration of distant regions brought new knowledge of their faunas and floras, the tremendous number and variety of kinds of organisms came to be more fully appreciated, and it eventually became certain that most of the fossil types were no longer living anywhere on earth. Comparative anatomical studies were revealing a multitude of concealed but fundamental resemblances between superficially unlike animals and plants; and unexplained likenesses were being found between the early embryonic stages of animals that differed greatly as adults. The doctrine of special creation offered no satisfactory explanation of these and great numbers of other new facts, which were to fall so neatly into place and acquire so clear a significance under the theory of evolution.

More and more persons came to feel that these phenomena must have some meaning, if it could only be grasped; and by the latter part of the eighteenth and the first part of the nineteenth centuries, a number of biologists and naturalist-philosophers were seeking some consistent and adequate theory that would account for them. The earlier of these men were merely feeling their way, their ideas being very vague, incomplete, and speculative. In 1790, the great German poet Goethe put forth a "theory of metamorphosis" to account for the transformation of leaves into the parts of flowers; and between 1790 and 1815, Erasmus Darwin (the grandfather of Charles Darwin), in England, and Lamarck, in France, attempted to account for modern organisms by appealing to a long sequence of changes and modifications from more primitive ancestral stocks. By the second quarter of the nineteenth century, such evolutionary speculation had become rather general. In 1844, Robert Chambers, a popular Scotch essayist, in his *Vestiges of Creation*, made a number of very bold and stimulating suggestions as to the origin of present-day organisms and their relations to the fossil forms of the past. The poet Tennyson was probably influenced by the *Vestiges* when he wrote the following part of *In Memoriam*, sometime before 1850:

> Nature . . .
> So careful of the type she seems,
> So careless of the single life . . .
>
> . . .
>
> "So careful of the type? but no.
> From scarpèd cliff and quarried stone
> She cries, "A thousand types are gone;
> "I care for nothing, all shall go."

All this pre-Darwinian work suffered from two defects—an insufficiency of factual evidence that evolutionary changes had actually occurred and failure to show any adequate causes for such change. Biologists therefore found themselves in the predicament of having to abandon the idea of special creation because of its inadequacies, while there was still no acceptable alternative. The proof of the reality of evolution, the formulation of a theory capable of accounting for it, and the testing of this theory against the background of accumulated biological knowledge were the work of Charles Darwin, and constitute one of the great achievements of science.

THE ESTABLISHMENT OF THE FACT OF EVOLUTION

Charles Darwin was born in 1809. His education, in preparation first for medicine at Edinburgh and then for theology at Cambridge, gave him a very meager training in technical biology. By natural inclination, however, he became a good field naturalist, with a strong interest in geology as well as in animals and plants. He was particularly stimulated by Sir Charles Lyell's *Principles of Geology*, in which Hutton's concept of uniformitarianism had been made the basis for a new interpretation of earth history and processes. In 1831, shortly after he had graduated, when he was only twenty-two years old, Darwin was offered the unsalaried position of naturalist on board the British cruiser *Beagle*, which had been detailed to spend 5 years in making oceanographic charts for the British admiralty. Most of this period was spent in mapping the harbors and coastal waters of South America, and Darwin took full advantage of his unusual opportunity to study the fauna, flora, and geology of this continent. All the way from Brazil to Patagonia and thence up the west coast to Chile, he made extensive collections and recorded his observations, both along the coast and on long trips inland. Later, the ship spent some time at the Galapagos Islands, some 600 miles due west of Ecuador in the Pacific, and then returned around the world to England.

It was his detailed observations of the animal and plant life of South America, especially of the distribution of species on this continent and in the Galapagos Islands, that first convinced Darwin of the inadequacy of the doctrine of special creation and started him on the search for a satisfactory substitute. Returning from the voyage in 1836, he occupied himself with publishing reports on his observations, in bringing out a number of zoological researches that established his reputation as a first-rate biologist, and especially in striving to find an acceptable explanation of the diversity of organisms and the peculiarities of their distribution over the face of the earth.

In Darwin's own words:

> On my return home in the autumn of 1836 I immediately began to prepare my journal [of the voyage of the *Beagle*] for publication, and then saw how many facts indicated the common descent of species. . . . In July (1837) I opened my first notebook for facts in relation to the origin of species, about which I had long reflected, and never ceased working for the next twenty years. . . . Had been greatly struck from about the month of March on character of South American fossils, and species on Galapagos Archipelago. These facts (especially latter) origin of all my views. . . .
>
> In October (1838), that is fifteen months after I had begun my systematic inquiry, I happened to read for amusement *Malthus on Population*, and being well prepared to appreciate the struggle for existence which everywhere goes on, from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favorable variations would tend to be preserved, and unfavorable ones to be destroyed. The result of this would be the origin of new species. Here then I had at last got a theory by which to work.

Malthus had attempted to show that most of the social and economic ills of society come from too high a reproductive rate in man, and this concept furnished Darwin with the clue to many of the questions that had been puzzling him and served as the starting point for his theory of natural selection.

"The Origin of Species." For 20 years more, Darwin accumulated data from all fields of biology, sifting and testing it, making new observations and experiments, and looking always for facts that might disprove his hypotheses as well as for supporting evidence. Gradually he built up, on the one hand, a vast body of facts that demonstrated beyond question that evolution had occurred and, on the other, a theory of organic evolution that seemed to fit the known facts. During nearly all this period of intensive work, he was in ill health and lived the life of an invalid and recluse.

In 1857, he ventured to submit a draft of his theory to a number of his scientific friends for comment and criticism. The following year, he received a manuscript from Alfred Russel Wallace, a young naturalist who was studying the distribution of life in the Malay archipelago. Wallace, like Darwin, had been particularly impressed by the diversity and the peculiarities of distribution of living things, and he, too, had chanced to read Malthus. His conclusions, reached independently, were much like those of Darwin but had not undergone the searching criticism of 20 years' study. Wallace asked that, if the paper seemed of sufficient merit, Darwin should present it to the Linnaean Society, not knowing that the older man had been working along similar lines. Darwin might have done this, suppressing his own work, had not his friends persuaded him to make an abstract to present along with Wallace's paper at a meeting of the Linnaean Society in July, 1858. The joint paper created a tremendous turmoil—the first great debate on evolution. The following year, in November, 1859, *The Origin of Species* was published.

In many respects, modern biology may be said to date from the appearance of this work. Although some of the older biologists refused to accept evolution, it rapidly became established as one of the basic principles of biology—perhaps the most fundamental of all, since this single concept affords a common explanation and correlating factor for the findings from all fields of biological research. Its influence has been equally far-reaching outside the field of biology and has profoundly affected all science and philosophy.

The Proof of the Fact of Evolution. *The Origin of Species* actually did two distinct things, though they were not treated by Darwin as separate. First and most important, it presented proof that evolution has actually occurred. This proof consisted of thousands of laboriously accumulated facts that are understandable only on the assumption that the species of animals and plants are of common descent and have become different from their ancestors. This conclusion is now unquestioned by biologists.

The Theory of Natural Selection. In the second place, *The Origin of Species* offered Darwin's explanation of the mechanism of evolution. In formulating this theory, Darwin found his essential clues, first in the effects of artificial *selection* of variations occurring among domestic animals and cultivated plants and second in the concept (derived from Malthus) of *competition* for success in an overpopulated world. His reasoning was as follows:

1. *The Effects of Artificial Selection.* From a few original kinds of useful animals and plants, men have succeeded in producing a great number and variety of cultural races by breeding from those individuals that possessed the most desirable characteristics. As Darwin was aware, many of the improved varieties have appeared at a single leap as "sports"; but others (and Darwin believed these to be the more numerous) were obtained by breeding from those individuals of a variable stock that showed the beginnings of desired modifications, by crossing of strains, and by repetition of the selection through subsequent generations. Darwin transferred the idea of selective breeding to events as they occur without human intervention and sought for selective agencies at work on species in the wild state.

2. *The Theory of Natural Selection.* This, the essential part of the Darwinian explanation of the causes of evolution, rests upon the following propositions:

a. Overproduction of offspring. Animals and plants are enormously fertile; the young produced by each generation are many times as numerous as the parents. Yet the number of individuals of each species remains approximately stationary under natural conditions, showing that most of the offspring of each generation must perish.

b. The struggle for existence. Since more organisms are produced than can survive, there is *competition* between individuals for food and space. Also, since not all situations are equally well suited for a particular kind of organism, each individual must pass an endurance test set by those factors of the environment that are unfavorable to it. Which individuals survive and which ones die, depends upon the outcome of this struggle for existence.

c. Variation and natural selection. The different individuals of the same species are not all alike. Because of this variation, some will in one way or another be better fitted than others to succeed in the struggle for existence, and there will thus be natural selection of the more fit for survival and production of the next generation.

d. Hereditary transmission of characteristics. The survivors of one generation will tend to transmit their own characteristics to their progeny, including those characters that ensured their own survival. The less fit, most of which will die while young, will in the long run fail to reproduce themselves.

e. Continued change inevitable. Because of this natural selection, each new generation will show an appreciable increase in average fitness to the environment. But since overproduction of offspring and the struggle for existence operate anew on each successive generation and since the physical environment does not remain fixed, *complete adaptation can never be reached,* and continued change must result.

f. Formation of new species (speciation). Not only will the descendants of one stock change as time passes and thus become different "species" from their ancestors but also, if some of the members of this stock meet the conditions of life through change in one direction and others through change in other directions, the different groups must end by becoming *different species,* though descended from a single ancestral species.

g. Nonadaptive characters. Variations that prove neither useful nor harmful to their possessors will be unaffected by natural selection and will remain as fluctuating variations about an unchanged average condition.

3. *The Theory of Sexual Selection.* Darwin saw that there were differences between the sexes of many species (for example, plumages of male and female birds, presence or absence of antlers in deer, etc.) which could not be adequately accounted for by the theory of natural

selection. In an effort to explain such differences, he developed the theory of sexual selection, in which competition for mates (through combats between males or choice exercised by the females) determines success in mating, and this is added to natural selection as a factor responsible for change. This is a subsidiary theory with which we shall not further concern ourselves in this book.

We shall return to an examination of the present status of the theory of natural selection after having reviewed some of the evidence establishing the fact of evolution. It may be noted at this point that the terms *evolution* and *Darwinism* are not necessarily synonymous, though they are often so used; many biologists reserve the latter for Darwin's explanation of the causes of evolution. Irrespective of the final fate of his theory of natural selection, Darwin's unanswerable demonstration that *evolution is a historical fact* suffices in itself to rank him as one of the outstanding men of science and perhaps the greatest of biologists.

CHAPTER XXV

Evidences of Evolution from Living Organisms

In undertaking to "review the evidence" that has convinced biologists of the truth of evolution,[1] it should at once be made clear that we are not engaged in argument but in seeking to know and understand the facts. The argument over evolution is long since concluded. Choice of this particular method of presenting the data has been made partly because it is a logical continuation of the historical approach of the preceding chapter and partly because it aids in bringing out the significance of the facts to be discussed. We may well start by considering just what is meant by organic evolution and by looking at some of the assumptions we shall have to make in dealing with the evidence.

Definition of Organic Evolution. Perhaps, in the present state of our knowledge, it would be better to speak of a description than of a definition of organic evolution, even though we do begin to have some understanding of this really very complex biological phenomenon. Viewed broadly, evolution can be summed up in a phrase—"descent with modification"; or the definition can be expanded into a more detailed and explicit statement of the observed facts. The basic generalization may be phrased thus: *The species of animals and plants living today* (*or at any period in the past*) *were not created as separate kinds but have descended, with changes in form, structure, and habits, from fewer and, in most instances, simpler kinds of ancestors.* This is a biological phenomenon—a fact which requires explanation and which itself accounts for otherwise inexplicable features of organisms.

Discovery of the fact of evolution considerably antedated the founding of the science of genetics, but today we can see that evolution is a logical and inevitable result of the principles of that science. It represents the summation of the effects of heredity with variation, operating through vast periods of time and in relation to slowly changing environments that have limited and thus, in a sense, controlled the changes that have occurred in organisms. To many people, the word *evolution* conveys distorted or erroneous ideas and connotations, which involve their religious beliefs and emotions, whereas actually evolution is an impersonal biological fact as unrelated to individual human hopes and aspirations as the law of gravitation.

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[1] In what follows, the term *evolution* is used as though it were synonymous with *organic evolution.* Strictly speaking, of course, it has a much broader meaning than this. Evolution in general implies a gradual unfolding, working out, or growth, and besides its special application in biology it is in frequent use to designate any type of orderly developmental sequence or process.

The basic generalization just stated has two important corollaries, both of which may be regarded as amplifying our definition of organic evolution. These are (1) that with the passage of time, single species tend to split up and form more than one species; and (2) that there must be "blood relationships" in varying degree among all organisms. Since these two points are important, they may be a little further elaborated.

The Multiplication of Species. In spite of the strong tendency that exists for each plant and animal species to breed true from generation to generation (*heredity*), we have seen that new characteristics do appear from time to time, so that offspring are produced that are unlike their parents in some respects (*heritable variations*). Slow accumulation of such variations through thousands of generations makes the living populations ever more different from their increasingly remote ancestors. Furthermore, if any factor operates so that one group of descendants accumulates variations, many of which differ from those accumulated in another set of descendants, the two groups will end by being different not only from the common ancestral population but also from each other.

A variety of isolating factors, to be discussed later, are known to have this result. It is therefore not surprising to find from the fossil record that over long periods of time the descendants of a single original stock not only have become different from their ancestors but have usually split up into several or many kinds. More and more species of organisms have thus continually been coming into existence, and the number of species existing today would be enormously greater than it is had all of them been able to survive. Actually, the majority of those produced have sooner or later become extinct. The whole evolutionary process of gradual change, with branching out and splitting up of stocks and the continual dying out of multitudes of species, has evidently been in operation since the beginning of life, since we find its records from as far back in time as fossils have been preserved.

The Blood Relationships of Organisms. If the species living today have arisen by the splitting up of older species and those, in turn, by the same process, ad infinitum, it follows that all the multitudinous divisions of life—both species and individuals—must actually be related by blood ties in the same sense that human cousins are said to be so related.

Of course, the relationship between any two species is very much more remote than that which exists between individuals of a single species, but it is based on the same fact of descent from common ancestors. To find the common ancestor of related species, we must usually look back some thousands or even a million or so years; the common ancestors of species belonging to different genera of one family are still more remote in time; and the common origins of the animal and plant phyla for the most part antedate the beginning of the geological record and must be assumed on the basis of indirect evidence. In general, the more similar two organisms are to each other the more recently they have separated out of an ancestral stock common to them both, and hence the more closely they are related. There is a strong probability that life arose only once on this planet and that all the phyla of plants and animals are the descendants of the original protoplasm. If this belief is well founded, then every living thing is related to every other living thing by blood ties, remote through they may be.

Some Necessary Assumptions. Unless it is called to our attention, we are likely to forget that we continually make and act upon assumptions—untested or untestable beliefs. In science, such assumptions are kept to a minimum by testing and verifying all hypotheses so far as it is possible; but there comes a point beyond which verification cannot go, and assumption becomes the only remaining basis of procedure. This is not the place to discuss the assumptions that underlie all science and even the possibility of knowledge itself. Here we wish merely to call attention to a basic scientific assumption, which is taken for granted in dealing with physical phenomena but is sometimes ignored in dealing with evolution, and to mention briefly another assumption of a biological nature. The first is a belief in the *consistency of nature.* This is merely a way of saying that we assume that phenomena are governed by law and hence are orderly and at least theoretically predictable; that they are related in dependable sequences that we speak of as cause and effect; that there is no caprice or exception; that miracles do not occur. The second assumption is of a very much more special and limited character. It is that *all fundamental similarity* (*homology*) *rests upon kinship,* not only in those instances where this can be demonstrated (as in short sequences of generations) but in all other cases as well.

The Nature of the Evidence. Organisms themselves show that they are the products of evolutionary change, and the evidences of evolution are coextensive with our knowledge of animals and plants. We shall deal briefly with the facts of structure, or *morphology,* with the phenomena of development, or *embryology,* and with matters of function, or *physiology,* to show how each of these subsciences furnishes clear evidence that evolution has occurred. We shall then turn to *classifica-*

tion, geographic distribution, and *paleontology* and see that not only do these contribute additional evidence of the truth of evolution but that they can, indeed, be understood only in the light of this doctrine.

THE EVIDENCE FROM COMPARATIVE MORPHOLOGY

If organisms are in fact related, it is reasonable to suppose that the closer the degree of relationship between any two species the more characteristics they will possess in common. Therefore, one of the most evident approaches to the question of relationship is to discover whether organisms do show such graded degrees of resemblance as we should expect to find if evolution has occurred. This involves the making of detailed comparisons, organ by organ and part by part, of as many different kinds of animals and plants as possible. In carrying out this program, we do, of course, encounter resemblances among organisms on every hand; but we also learn to be cautious about accepting any and every case of resemblance as evidence of relationship. Critical consideration shows that the similarities are of two different sorts, one of which (*homology*) is accepted as showing direct relationship and the other (*analogy*), as showing convergence between only distantly related (so-called "unrelated") forms. In making this distinction, we are not selecting evidence that fits the case that we wish to prove, as might be claimed; on the contrary, the distinction between these two sorts of resemblance is easy to understand, though it is not always so easy to apply to a particular instance. We may begin by considering clear-cut examples of the two classes, and later we shall see how both concepts, homology and analogy, may enter into other cases of resemblance.

Analogy. When, in different organisms, we find structures that look alike and have similar functions but that differ both in structural plan and in origin, such structures are said to be *analogous,* or to show analogous resemblance. Similarities of this sort are often encountered in very different organisms, which no one would mistake for close relatives. Thus both moles and mole crickets possess digging feet that are surprisingly similar in general form. Yet the mole is clearly a mammal, and its digging foot is built on the same basic plan as the arm of a man; the digging tools are the strong, flattened claws at the ends of the digits. The mole cricket, on the other hand, is an arthropod; its digging foot is a modified insect leg, and the digging prongs are mere spinous projections of the exoskeleton. The similarity between the two organs is altogether superficial and extends neither to the details of construction nor to the underlying structural plans upon which they are built.

The jumping legs of kangaroos and grasshoppers are analogous but are so unlike in structure that here again there would be no chance of assuming a relationship where in fact none existed. Other equally obvious instances of analogy are: the wings of butterflies and those of birds (the former a hinged fold of skin strengthened by longitudinal thickenings of the exoskeleton, the latter a modified vertebrate arm); the "poison fangs" of snakes and of spiders (the snake fang a modified tooth, the spider "fang" a modified arthropod leg): and the jaws of vertebrates and of insects (the first formed by a vertically hinged part of the skeleton of the head, with its enclosing tissues; the second, by a pair of laterally hinged modified appendages). Thus we see that organs may be analogous without being very similar in form; or they may be quite similar in superficial appearance but be associated with other characteristics that make it obvious that there can be no close relationship among the organisms that possess them.

On the other hand, analogous resemblances are often so close that, until critically examined, they may easily be mistaken for homologies. As illustrations, we may cite the close superficial likenesses between the tails of fishes and those of whales, the streamlined bodies of sharks and porpoises, the bivalve shells of clams and brachiopods, the creeping soles of snails and certain caterpillars, and the eyes of vertebrates and of cephalopod mollusks. In all these instances, the resemblance is very close, but put to the test of structure and mode of origin, they all prove to be merely analogous features adapted for the performance of identical tasks. A close resemblance exists between certain small burrowing lizards (Amphisbaenidae) and a group of small burrowing snakes (Typhlopidae, "worm snakes"), because the former have lost their legs, and both groups have become blind and have short tails. These external similarities have evidently arisen by convergent evolutionary modifications that occurred independently in the two groups and for this reason are not an indication of relationship.

Homology. When, in different organisms, we encounter structures that have similar origins and are built on the same fundamental plan, such organs are said to be *homologous* or to show homologous resemblance, irrespective of whether or not they are similar in appearance and are of like function. No one can doubt that the foreleg of the dog and that of the wolf are homologous, for not only do they arise in the same way and have the same basic structure but also they agree even in minor details. They are completely homologous. In other instances, two organs may differ moderately in details, while the fact of their homology remains wholly apparent. Thus the foot of man and of gorilla are built on the same pattern; they agree in the number, shape, and arrangement of the bones and in the disposition of muscles and tendons and differ chiefly in relative length of digits and degree of opposability of the great toe. They are homologous in all except minor details.

In still other instances, organs that are adapted to entirely different functions and that differ strongly in appearance may prove to be constructed on a common plan. One of the most clear-cut instances of homology is that which exists among the forelimbs of vertebrate animals (arms, wings, forefeet, swimming paddles, etc.). In this classic case, the underlying structural resemblances are so evident, in spite of the superficial dissimilarities, that the various structures could safely be judged homologous without reference to embryological or paleontological evidence. The skeletons of the forelimbs of man, bat, bird, cat, horse, seal, and whale correspond very closely, bone for bone, at most points. So many similarities could scarcely be the result of accident or of convergence from originally distinct types of structure; the only reasonable interpretation is that the forms showing the likenesses are all related. To the extent that these different limbs represent mere modifications of the same structural plan—the *pentadactyl* (five-fingered) *vertebrate limb*—they are all homologous, though modified to serve various functions.

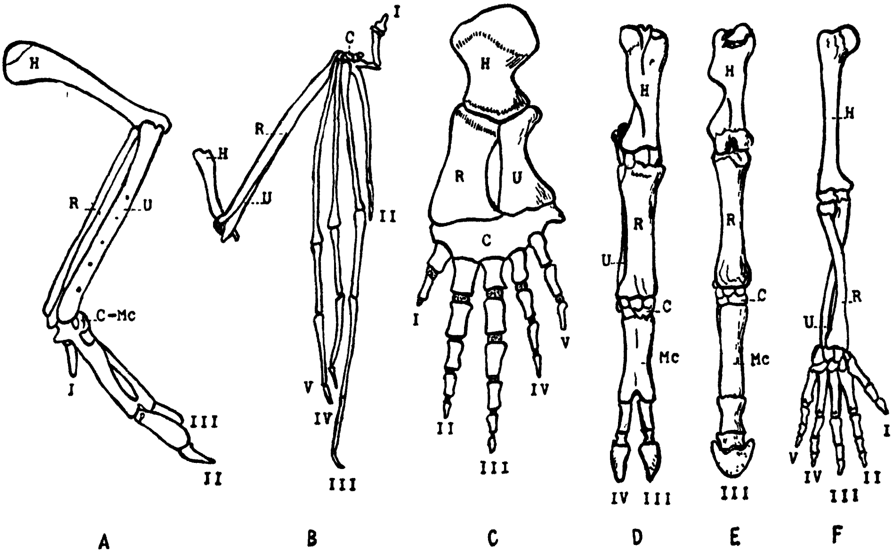

Fig. 112. *Homologies between the bones of the forelimbs of various vertebrates.* (*A*) *Left wing of a bird;* (*B*) *right wing of a bat;* (*C*) *left flipper of a whale;* (*D*) *right foreleg of an ox;* (*E*) *right foreleg of a horse;* (*F*) *right arm and hand of man.* (*C*) *Carpals;* (*H*) *humerus;* (*Mc*) *metacarpals;* (*R*) *radius;* (*U*) *ulna;* (*I–V*) *digits.* (*From Scott, The Theory of Evolution, The Macmillan Company.*)

Relations between Homologous and Analogous Resemblances. From what has just been said, it is evident that we must recognize different degrees of homologous resemblance. Only in the instance of almost identical structures is it justifiable to speak of them as being

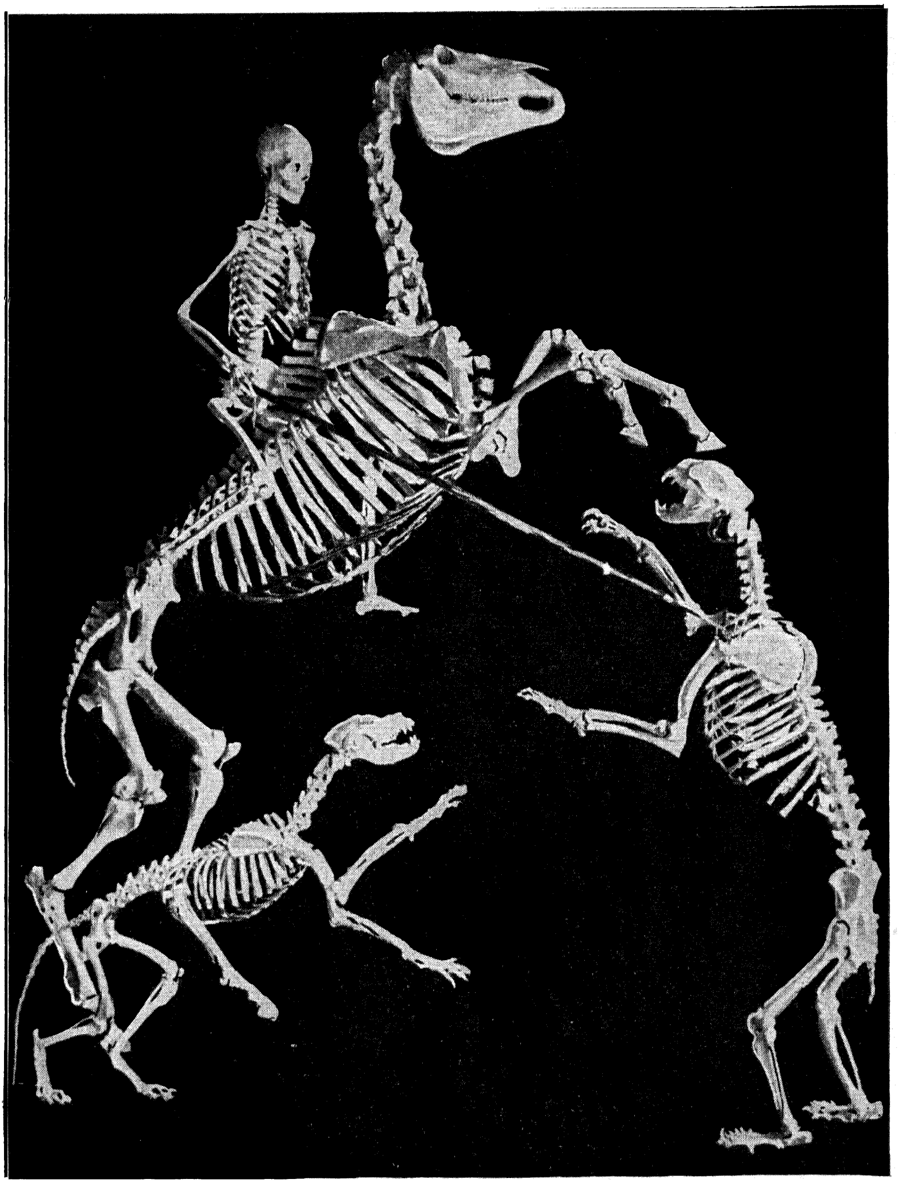

FIG. 113. *Skeletal homologies in mammals, as illustrated by "The Bear Hunt," designed and mounted by Charles H. Ward for the Chicago Fair of 1893. (Courtesy of Ward's Natural Science Establishment, Inc.*

entirely homologous; instead it is generally necessary to say that the structures are homologous *in respect to certain features.* This distinction needs to be understood clearly, since it not infrequently happens that two structures may be homologous in fundamental plan and at the same time merely analogous in respect to superficial characteristics. Thus the wings of birds and of bats are both modifications of the pentadactyl vertebrate limb and to this extent are strictly homologous with each other and with the forelimbs of terrestrial mammals, reptiles, and amphibians. The particular features that adapt them for flight, on the other hand, are essentially unlike and evidently arose independently in two stocks, both of which possessed the pentadactyl limb as a starting point. In the bats, the flying surface is a thin membrane of skin stretched between the outspread and elongated digits; in birds, the flight surface is formed of skin appendages, the feathers, attached to an arm of which the digits are partially fused or lost. With respect to the flight adaptations, therefore, these two limbs are merely analogous in spite of their more fundamental homology. Similar analogous modifications of basically homologous structures are not at all uncommon. As examples, we may cite the digging adaptations in the forelegs of the true mole (an insectivore) and the Australian mole (a marsupial); the lobes on the feet of certain water birds, the coots, phalaropes, and grebes; the elongation of the body and loss of legs in snakes and certain lizards; and the paddlelike forelimbs of penguins and of seals.

The Significance of Homology. As we have already noted, it has become axiomatic in biology that *all homology rests upon relationship,* since this is the only interpretation of the phenomenon that affords a working basis for its evaluation. It is not, however, wholly an assumption; homologous resemblance is most complete among the individuals of a single species, where blood relationship is closest, and becomes less and less in degree as one compares organisms that, by other criteria (physiological, embryological, and paleontological), seem less closely related. If degree of homologous resemblance does indicate degree of relationship, it can be used to build up a natural classification of organisms along phylogenetic lines. For example, the forelegs of horse, zebra, and dog are all to some extent homologous, but the first two resemble each other more closely than they do the third. This, together with much additional evidence from morphology, embryology, and blood tests, indicates that the relationship between the horse and zebra is relatively close, whereas horse and zebra are both much more distantly related to the dog.

It is sometimes difficult to determine from present indications whether the presence of similar structures in two groups of animals indicates descent from a common ancestor or whether the groups have converged for some reason from originally distinct beginnings. In general, when groups of organisms have only one or a few structures in common, most or all of their other features being different, it is best to assume that the common structures arose independently through convergent evolution, at least so far as their recent evolutionary history is concerned. If, however, a great many features of two groups of organisms are closely similar, the probability is strong that such similarities could have come about only through descent from common ancestors. From this standpoint, we may say that homologous characters are those that have arisen in the same way in evolution. We shall see how the data of embryology furnish a more immediate basis for the recognition of homologies.

The Significance of Vestigial Structures. Since rudimentary or vestigial structures are useless or sometimes even detrimental to their possessors, they can scarcely be taken as evidence of design or purpose in the organic world. The only reasonable explanation for their existence is that they are *remnants* of organs that were once functional but are so no longer, especially since they are homologous with corresponding structures that are still functional in related organisms. The existence of vestigial structures is evidence that the organisms that exhibit them have changed in structure and in function, *i.e.*, have evolved.

Vestigial Structures Present in Man. The human body has numerous more or less completely vestigial structures, as many as 180 having been recognized by some authorities. Certain of these are present in all individuals during all or parts of their lives, but others are found in only an occasional person. We shall discuss first some of the better known examples.

The *hair* on the human body is vestigial, since it no longer serves its original function of preventing the loss of heat. The small *hair-erecting muscles* in the skin are also vestigial organs. In animals with furry coats, they aid in retaining body heat by raising the individual hairs and thus increasing the thickness of the insulating layer of still air that is held above the skin by the forest of hairs. When the human skin is chilled, the little hair muscles contract and lift their individual hairs just as they do in other mammals but with no result other than to produce the phenomenon that we call goose flesh or goose pimples. The *arrangement of the hair* on the body may likewise be a vestigial characteristic. The hair on our upper arms points downward toward the elbow; that on our forearms runs upward toward the elbow. This is not the usual arrangement of hair on the limbs of mammals, but it does correspond with the arrangement found in the monkeys and great apes. It has been suggested that in these animals, which commonly sit with the arms over the head during storms, the disposition of the hair on the arms may help to shed rain from the body. Whatever may be its significance in the monkeys and apes, this same arrangement of the hair of the human arm has no functional importance and is meaningless except as it constitutes another small bit of evidence of the common heredity of these groups.

The ear is another part of the body that shows numerous vestigial features. The entire *outer ear* is so greatly reduced in size and so ineffective as a funnel for concentrating sound waves, compared to its development in many of the lower mammals, that it must itself be regarded as a vestigial organ. Most of us cannot move our ears, but a few gifted persons have this ability. Muscles for moving the ears are well developed among many mammals, but in man, although a complete set of these *ear muscles* is always present, they are only rarely functional and then only to a limited degree. Another vestigial structure that is occasionally present in the ear is *Darwin's point,* a small conical projection from the inrolled upper margin of the ear, which Darwin showed to be homologous with the pointed tip of the ear of lower mammals, now folded down and inward and reduced in size. Darwin's point is found in a small proportion of human beings and is likewise present as a vestigial structure in several of the apes.

The small crescent-shaped fold of skin in the inner angle of the eye is a vestigial homologue of the membranous third eyelid found among many lower forms, including such mammals as the cat. Here again it is of interest to note that among the great apes this third eyelid rudiment is as much reduced as in man.

The "wisdom teeth," or last molars, are in man approaching a vestigial condition, since they generally do not appear until relatively late, between the ages of twenty and thirty years, and in many persons are never cut at all. In a large percentage of individuals, they are useless, and they often become impacted and have to be removed surgically. The human *appendix* is another vestigial organ, which, as everyone knows, may be a source of danger to its possessor. It is a rudimentary homologue of the large pouch or caecum that forms a part of the large intestine in many of the herbivorous mammals and that in them is a functional part of the digestive tract. The presence of this useless and dangerous organ in our anatomy is inexplicable except as an inheritance from ancestors in which it was useful. Likewise, it is impossible to see in the *coccyx* anything but a diminutive and abbreviated vestigial tail, buried in the tissues between the buttocks in the great apes and man but homologous with the projecting tails of other mammals.

The examples of vestigial structures just cited are among the more obvious and better known ones, but the human body is full of such leftovers. Two less obvious ones are here described. The first has to do with the *relation of the lungs to the heart and diaphragm.* In mammals that walk on all fours, there is a space between the heart and the diaphragm, and this space is occupied by a special lobe of the right lung. In upright animals such as man and the great apes, the heart comes to rest upon the diaphragm, filling the space; the right lung no longer has the special lobe, but a rudiment of it can always be seen, and this rudiment sometimes projects between the heart and the diaphragm. It is reasonable to conclude from these observations that the lung originally possessed such a lobe, that there must therefore originally have been a space between the heart and the diaphragm, and hence that the apes and man have descended from ancestors that walked on all fours. The second example relates to an inconspicuous anatomical feature of the arm. In many reptiles and primitive mammals and in some of the lower primates, the upper armbone (humerus) has a small opening (foramen), covered by a bony arch on the inner side just above the elbow; through this foramen, the main artery and nerve of the arm pass. In man and the higher apes, the foramen is not present, and the artery and nerve simply lie alongside the bone; but not infrequently, the humerus develops a small hooklike process at a point corresponding to the locus of the foramen, and when this is the case, the artery and nerve pass under the process. Very rarely in man, the bony arch is found complete, with artery and nerve passing through the foramen it forms. The occasional appearance of this minute and inconspicuous bony part, either as a complete or an incomplete arch, is inexplicable except on the hypothesis that the structure has been inherited as a vestige from ancestors in which the nerve and artery normally passed through a foramen on the humerus.

Some of the more interesting vestigial characters are present only in the embryo or in early infancy, and it is to comparative embryology that we must turn for an interpretation of the full significance of these as well as of the examples given above. Before taking up the evidence from that field, however, we may consider briefly a few of the vestigial structures of the human embryo and the occurrence of vestigial organs in other animals than man.

In the course of its development, the human embryo acquires many structures and characteristics that later are normally lost or almost unrecognizably altered. Some of these, such as the embryonic membranes and the placenta and cord, are obviously related to the requirements of embryonic existence and need no other explanation; these are clearly not vestigial structures. Other temporary embryonic structures fall into two classes; some are purely vestigial, apparently as useless as many of the vestigial organs present in the adult; others, though in a sense vestigial, play essential roles in the attainment of adult structure and are not at all in the same category as ear muscles or hair pattern. We have space to describe only a few examples of vestigial embryonic characters.

The human embryo has a well-developed tail, which, interestingly enough, is formed complete with muscles for wagging it. Normally, the tail lags behind in development, forming only four or sometimes five vertebrae that make up the coccyx; these curl under and help to close the opening in the pelvis and support the viscera. As the tail fades into insignificance, the muscles degenerate or are turned to other uses. The great apes have proceeded even farther than man in the loss of the tail, retaining only two or three instead of four or five tail vertebrae. Very rarely in man, the embryonic tail fails to curl under and degenerate but persists and even enlarges, forming a short but unmistakable external tail up to several inches long in adults.

In the early human embryo, the nostrils are connected with the mouth by a deep groove on either side. This is a vestige of the condition that may still be seen in the adults of such fishes as the shark and the ray. In normal embryonic development, this groove later closes, and the upper lip is formed as a complete structure. Occasionally, however, the groove fails to close, and the condition known as harelip is produced. The body of the embryo between the sixth and eighth month is covered with a coat of hair called the *lanugo*, which is usually lost before birth; this can be regarded only as a temporary reproduction of a condition that was permanent among some of our ancestors. Occasionally this embryonic hair persists as a more or less complete hairy covering of the body of the adult; this is the explanation of the hairy freaks of the side shows, who merely retain a coat of hair that most of us lose before birth.

The striking ability of the newborn infant to hang and cling by means of its hands is almost certainly another example of a vestigial characteristic. Shortly after birth, a baby is capable of supporting its own weight for several minutes at a time, hanging by the hands alone; indeed, in many cases, the child can hang by either hand separately. This capacity lasts for some weeks or a month after birth, after which it is lost. In view of the known fact that the young of arboreal primates must cling to the hairy coat of the mother while she makes use of her hands and feet in climbing, this suggests that the ancestors of human beings were similarly unable to carry their young and that the latter had to be able to cling to their mothers for support.

Vestigial Structures Present in Other Animals. Man is far from unique in possessing rudimentary and useless organs. Such structures may be found among all groups of animals, but known examples are especially numerous among the vertebrates, partly because these animals are more complicated than most others and hence give greater opportunity for the development of vestigial organs, and partly because they have been the most thoroughly studied. Among the more striking examples shown by vertebrates are the following: the rudimentary pelvis and hind legs of the whales, the vestigial hind legs of the python, the fused fingers in the wings of modern birds, the rudimentary wing bones in certain flightless birds, and the blind eyes of many cave animals. As examples of rudimentary structures among invertebrates, we may cite the useless abbreviated wings of many grasshoppers and other insects, the traces of legs on the abdominal segments of the most primitive insects, the rudimentary shells buried in the tissues of such mollusks as slugs and squids, and the reduced and practically nonfunctional anus in such echinoderms as sea urchins and starfishes.

THE EVIDENCE FROM COMPARATIVE EMBRYOLOGY

Embryology—the study of the developmental stages of individual organisms—although it constitutes a special field of biology, is so intimately related to comparative anatomy that it is difficult and somewhat arbitrary to separate the two fields; the matter presented under these two heads therefore overlaps to some extent. The evidence from embryology falls into two categories: (1) *the resemblances between embryos of different groups* and (2) *the resemblances between embryos of the higher groups and adults of lower groups.* In the following discussion, we shall confine our treatment to animals, since they illustrate the phenomena more clearly than do plants.

If we were to start with 1,000 different zygotes, selected proportionately from the various animal phyla (see Fig. 114), we should find that, although they differ in size and in the amount and distribution of yolk, all agree in being single cells that show no indication of the kind of adult animal that is to develop from any one of them. All of them undergo a rapid subdivision, or *segmentation,* which results in formation of what is essentially a hollow ball of cells, the *blastula.* A few colonial Protista, such as Volvox, proceed as far as this stage and, as fully developed colonies, correspond in structure to the blastulae of the higher animals. The blastulae of all the Metazoa, however, must continue through further embryonic development.

Nearly all of them undergo an infolding or invagination by which each becomes a gastrula. (The blastulae of sponges do not develop into true gastrulae but show a somewhat different type of infolding and rapidly transform into two-layered adult sponges.) Among those embryos that become gastrulae, a few soon transform into adults without radical structural alteration. These are all coelenterates (Hydra, corals, jellyfishes, etc.), in which the body is composed only of ectoderm and entoderm layers of cells, separated by a nonliving jellylike substance. They have a single gastrovascular cavity with a single opening, the mouth; these structures correspond to and are derived from the central cavity and blastopore of the gastrula, respectively.

Each embryo in the diminished company that remains proceeds to develop a third layer of cells, the *mesoderm,* between the ectoderm and entoderm layers, thus becoming *triploblastic.* A few (comb jellies and flatworms) drop out of the procession at this point and become triploblastic adults with a single body cavity and one opening to the exterior. All the others continue their development; but from this point on, they follow divergent paths, of which, for illustrative purposes, we need follow only two—that taken by the segmented worms and arthropods on the one hand and that taken by the chordates on the other.

In the embryos of each of these groups, a new body cavity (the *coelom*) is formed within the mesoderm; the body elongates and becomes subdivided into a series of similar repeated segments, the *somites;* and a central digestive tube with anterior mouth and posterior anus is formed. But in all other respects, the two groups develop along quite different lines.

1. In the first (*annelid-arthropod*) group of embryos, there appears a ventral nerve cord having segmentally repeated nerve centers, or ganglia; a tubular circulatory system is also formed.

From this basic condition, the embryos differentiate along divergent lines.

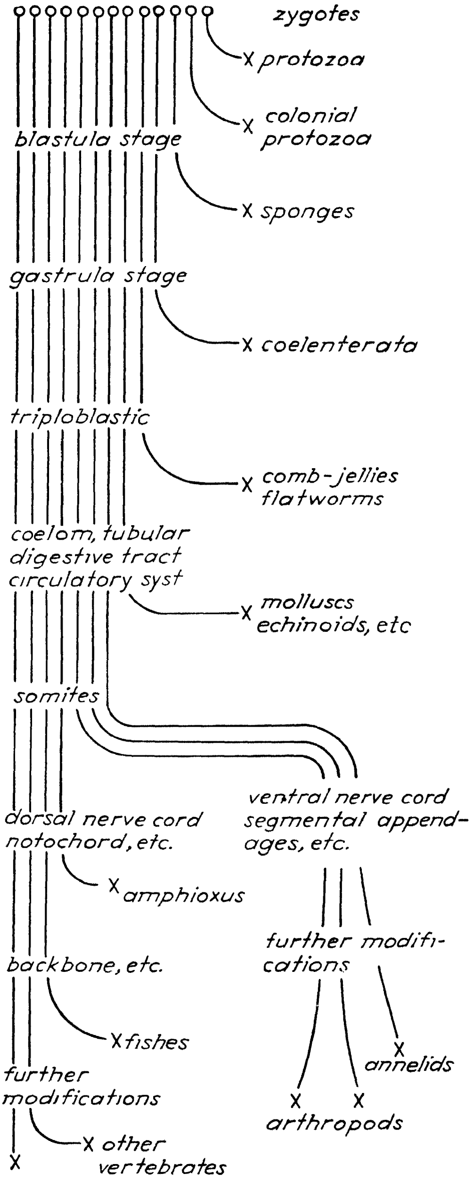
zygotes
X protozoa
X colonial protozoa
blastula stage
X sponges
gastrula stage
X coelenterata
triploblastic
X comb-jellies flatworms
coelom, tubular digestive tract circulatory syst
X molluscs echinoids, etc
somites
ventral nerve cord segmental appendages, etc.
dorsal nerve cord notochord, etc.
X amphioxus
further modifications
backbone, etc.
X fishes
X annelids
further modifications
X X arthropods
X other vertebrates
X

FIG. 114. *Diagram illustrating parallelisms and recapitulation in embryonic development.*

a. In one such line (*annelid*), the coelom remains extensive, the circulatory system continues as closed vessels, the number of somites greatly increases, and each somite typically forms a pair of fleshy, jointless lateral outgrowths, or appendages. Embryos that take this course develop into adults of various annelid worms. The last characters to appear are those which distinguish the different kinds of these worms.

b. In another line (*arthropod*), some of the blood vessels swell and fuse to form a huge blood cavity, which surrounds the digestive tract and largely takes the place of the much reduced coelom; a dorsal blood vessel that does not take part in this process is left to form a dorsal heart and aorta; a semirigid external skeleton is formed from the skin; and lateral outgrowths from certain of the somites become jointed appendages. Embryos that follow this path develop into adult arthropods of various sorts.

2. In the second (*chordate*) assemblage of embryos, the main nerve cord forms along the dorsal side, with a concentration of nerve tissues at the anterior end. The heart develops ventrally; the somites become intimately fused together; a stiff rod of cartilage, called the *notochord* ("back" + "cord"), appears beneath the dorsal nerve tube; and the neck region becomes perforated by a series of *gill slits* leading from the exterior into the gullet. This group, which includes the vertebrates and their allies, derives its name, *Chordata*, from the presence of the notochord.

Some of these embryos transform into adults at about this stage and never develop a backbone. The adults are wormlike or vase-shaped marine creatures, whose kinship to the vertebrates might have gone unrecognized had it not been for the features that their embryos share with those of the backboned animals. The great majority of the Chordata, however, are vertebrates, and their embryos undergo further development, during which the notochord is replaced by a series of bony structures that become the backbone. The vertebrates, in turn, are subdivided into the fishes, amphibians, reptiles, birds, and mammals, and the embryos of each of these groups now show their own special type of development. The embryos of the fishes have a shorter series of special modifications to undergo in arriving at adult structure than do those of amphibians, which must pass through most of the stages shown by the fish before they develop their peculiar amphibian characters; the embryos of the reptiles, birds, and mammals (amniates) have a still longer series of embryonic changes that carry them well past the amphibian stage of organization.

In the case of chordate embryos, we find (as we should in the annelid-arthropod or any other major group) that the characteristics that differentiate the classes in general appear before those which separate the orders, those of the orders before those of the families, etc. Broadly speaking—there are exceptions—the differences between similar species (for instance, dog and wolf) are the last to appear.

We may summarize the facts of comparative embryology by likening the course of development of each individual to the path of a vascular bundle in a tree and the degree of adult structural complexity to the height of the branches and twigs above the ground. Up to a certain level, the trunk has only a few small branches, but beyond this point it divides into several main limbs (phyla), each of which is subdivided into a large number of branches and twigs. In the trunk, multitudes of bundles run upward together; but at all levels, groups of them split off and run out into the branches, in which the groups subdivide again and again. Those bundles which run together to the finest twigs may be compared with the individuals of a single species, whose development has remained parallel to the end; those large groups of bundles which enter the main limbs represent the great divisions of the animal kingdom, whose members have developed in a manner parallel to the members of other phyla up to the point where the limb branches off from the trunk and which continue the parallelism among themselves until the phylum limb itself begins to branch.

More formally, the following statements express the facts observed:

1. Simpler organisms undergo fewer embryonic changes to reach the adult condition than do more complex "higher" organisms.
2. In the members of a given phylum, the sequence of changes undergone by the embryo is, with few exceptions, invariable.
3. Within each phylum, the "higher" forms undergo transformations that are similar to and follow the same sequence as those observed in the "lower" forms.
4. Furthermore, these "higher" forms attain their greater degree of final complexity as the result of (*a*) the *addition* of new changes at the end of the sequence and (*b*) *modification* of the earlier embryonic stages that they share with the "lower" forms.

Serial Homologies. The homologous resemblances between corresponding parts of different organisms are not the only ones that exist. Among metameric animals (of which the Annelida and Arthropoda are the most typical examples), the body shows serial repetition of somites (segments, metameres), each of which is a more or less modified replica of the others. The parts of these segments correspond and are said to be *serially homologous*. The repeated appendages show this homology most clearly. During the embryonic development of an annelid or an arthropod, the segments appear early, and each soon develops a pair of buds that are destined to become appendages. In many of the marine annelids, the buds develop into fleshy swimming

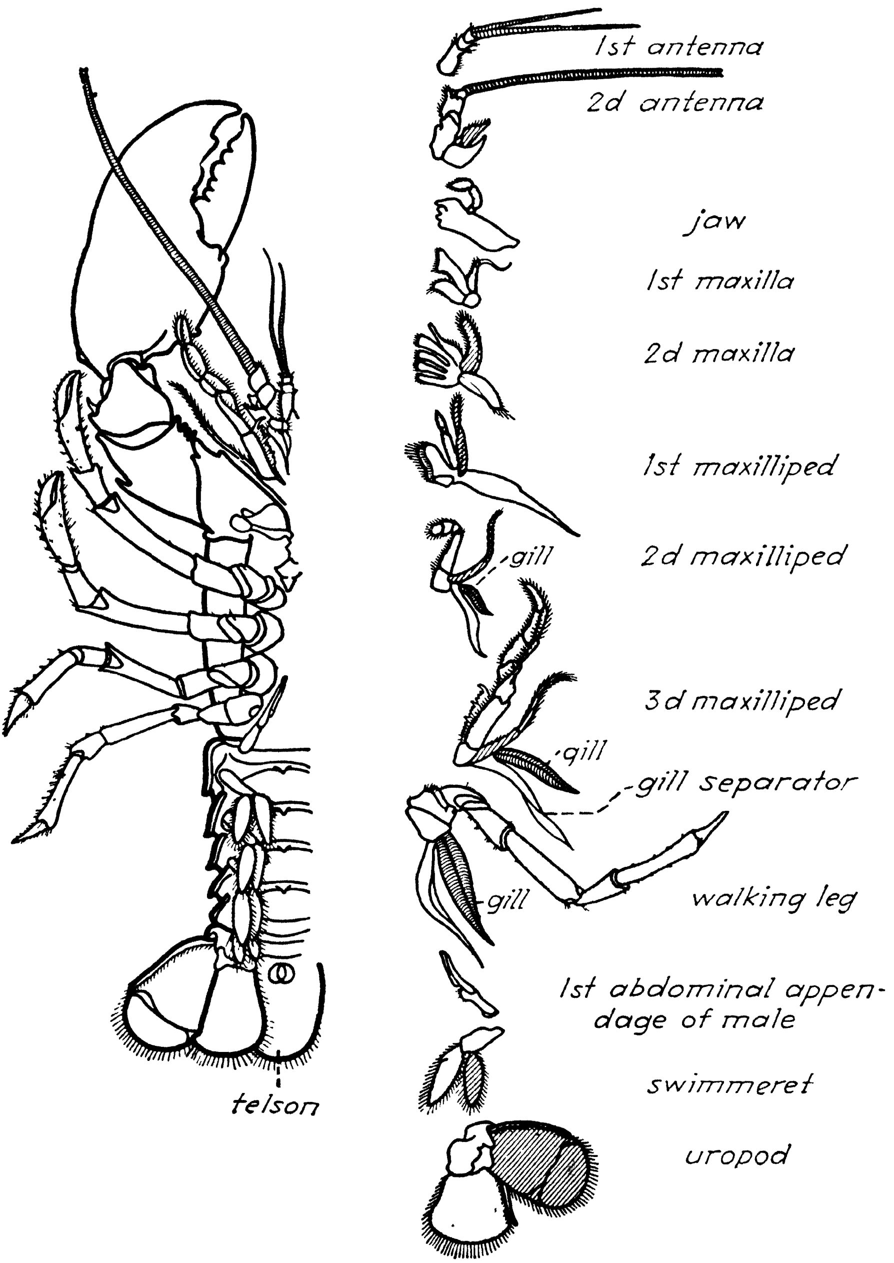
1st antenna
2d antenna
jaw
1st maxilla
2d maxilla
1st maxilliped
gill
2d maxilliped
3d maxilliped
gill
gill separator
gill
walking leg
1st abdominal appendage of male
swimmeret
uropod
telson

FIG. 115. *Serial homologies in the appendages of the lobster. These appendages show marked modifications related to their different functions, but they can all be reduced to a common basic plan. The inner branches are stippled, the outer branches are shaded with diagonal lines, and the basal piece and its processes are left unshaded. (From Buchsbaum, Animals without Backbones, University of Chicago Press.)*

organs which are almost duplicates of one another and which show their homology as clearly in the adult as in the embryo.

In the arthropods, however, some of the buds enlarge; others remain small or dwindle and disappear. Those that persist give rise to appendages that differ in appearance and function. In the crawfish, for example, they are variously modified into antennae, a series of mouth parts, a pair of large claw legs, smaller walking legs, small abdominal swimmerets, and a pair of flattened tail paddles used for swimming. Yet in spite of their superficial dissimilarity, these appendages are all built on a common plan and never occur more than one pair to a segment, because they arise from paired, segmentally arranged embryonic rudiments that arise in the same way and agree in position and structure.

Vertebrates are also metameric animals, though in this group the segments are fused and modified in the adult to such an extent that individual somites are scarcely distinguishable. Nevertheless, serial homology can easily be traced in vertebrates between such repeated parts as the vertebrae, ribs, and particularly the pelvic and shoulder girdles with their appendages. The latter correspond bone for bone, and this correspondence is again due to their origin from corresponding embryonic rudiments.

The fact that serial homology can be shown to result from differentiation of originally "identical" structures is good evidence that other homologies are to be interpreted in the same way.

In the light of these observations, we are in a position to re-examine the significance of homology and to consider another important and illuminating biological concept, recapitulation.

Homology Results from Common Origin. Homologous resemblances have already been defined and illustrated, and in that discussion mention was made of the light that embryology throws on their significance. We can now appreciate that the underlying resemblance between homologous structures results from the fact that such structures have developed from corresponding embryonic rudiments. One of the clearest proofs that this is the case is found in the development of serially homologous structures, as described in the preceding paragraph. The various degrees of modification that homologous structures show do not obliterate the basic similarities that result from their common origin. In applying the concept of homology, one must always be careful to distinguish between true homologies and the merely superficial (analogous) resemblances due to convergent evolution; the safest method of doing so is to trace the embryonic development of the two structures and determine whether or not they have a common origin.

Individual Development Recapitulates Racial History. We have just seen that, although there are as many different kinds of embryos as there are of adult animals, these embryos may be grouped on the basis of structure into fewer and fewer types as we proceed backward from the adult toward the single-celled stage. Furthermore, the facts of genetics strongly suggest that resemblance between two organisms results from the inheritance of similar gene combinations from common ancestors, and the resemblance between the embryos may be thus interpreted. Lastly, it has been shown that the "higher" organisms during their development pass through stages in which they resemble the adults of "lower" organisms and attain their final complexity only as a result of additional changes added to the end of the sequence. These and other facts are the basis for the *principle of recapitulation,* which states that, broadly speaking, the changes that every individual undergoes during its development from zygote to adult (*ontogeny*) run approximately parallel to the changes that occurred in the evolutionary development of its ancestral stock (*phylogeny*). The statement, "ontogeny repeats phylogeny" can, however, be regarded as true only in general and not in detail.

In the instance of the frog, the following structural resemblances can be noted between developmental stages and the adults of lower forms:

Zygote	Single-celled Protista
Blastula	Spherical colonial Protista
Gastrula	Coelenterate, such as Hydra
Very early tadpole	Primitive chordate, such as Amphioxus
Later legless tadpole	. Fish
Late tadpole with legs	Salamander
Adult frog (unique)	. .

Interpretation and Critique of Recapitulation. A developing frog is not successively a protozoan, Hydra, Amphioxus, fish, salamander, and finally a frog. It is truly a frog from the beginning, for a frog zygote can never develop into any other kind of animal. Yet the frog embryo exhibits striking correspondences with those of other vertebrates and also with the adults of "lower" organisms. We must account not only for the existence of such correspondences but also for the occasional failure of embryos to show expected resemblances and for the presence in certain animals of embryonic or larval features that do not occur either in their own adult stages or in the supposed ancestors. The following illustration is admittedly highly speculative, but it will show how the data from genetics is capable not only of enabling us to understand the significance of recapitulation but also of accounting both for the resemblances and for the differences shown by developing organisms.

Let us assume that hundreds of thousands of generations in the past, the ancestors of our frogs were fishes. (This much of the assumption is strongly borne out by all the available evidence from comparative morphology, embryology, paleontology, and historical geology.) These fishes reproduced their kind, according to the laws of heredity. We have seen that the characteristics of organisms are transmitted by the genes and that, although the genes are very stable, changes do take place in them from time to time, so that by mutation old characters are altered or new ones introduced. Although the number of genes that we can study at one time in genetics experiments is limited, it is certain that the total number of genes present in any organism is very large, and it is believed that all the characteristics of the organism are manifestations of the particular gene assemblage present in the single cell from which the individual develops.

Over great periods of time, the original *total genotype* possessed by the ancestral fishes was slowly modified by mutation. Some of the original genes may have been lost, others were perhaps only altered, and many new genes were doubtless added. Generation by generation, the descendants of the original fishes became ever more unlike their forebears, because their total genotype was changing; today they are frogs. Yet the total stock of genes of these frogs is merely that of the ancestral fishes, plus the modifications that this gene assemblage has undergone in the interim. The fishlike stage through which the frog passes results from its possession of fish genes inherited from its ancestors. The fact that it fails to become a fish and instead proceeds through additional stages of development to a more complex adult condition, is the result of changes and additions that have modified the original ancestral genotype into that characteristic of the frog.

Recapitulation is never complete and is often distorted. The resemblance of the embryos of higher organisms to their ancestral types is never exact but merely general, and the ontogeny often fails to show features known to have been present in the ancestors. Furthermore, immature organisms are frequently encountered which can scarcely represent, except in bare essentials of structure, any ancestral stage. Returning to our concept of evolution as the result of change in total genotype, we should note that *gene changes may affect the organism at any stage from germ cell to adult.* We must also recognize that developing organisms have *problems of maintenance* to meet, just as adults have; they must be adapted to their environments if they are to exist at all. Among the adjustments that embryos show are some that affect the rate of development and others that are related to maintenance in special environments.

1. *Rate of Development.* Individuals must develop from zygote to adult at a rate that is enormously rapid as compared with the slow process of evolutionary change. This "telescoping" of development is brought about partly by omission of stages, partly by overlapping of developmental processes; and these modifications sometimes result in altering the historical sequence of appearance of structures or processes. The embryonic record not only becomes condensed but becomes full of anachronisms as well. Thus, although the caterpillar (larva) of a butterfly corresponds in form and in many other respects to an annelid

stage of development, it possesses the respiratory air tubes characteristic of insects, which phylogenetically appeared relatively late and which no annelid possesses.

2. *Adaptations of Immature Stages to Environment.* Some embryos have developed special structures that enable them to feed upon a yolk supply furnished in the egg, and to carry on respiration and waste disposal within an eggshell. Obviously neither their ancestors, nor the adults into which they develop could possess such structures, which are embryonic organs superimposed on the inherited ontogeny. Other organisms become free-living in very early stages of development, as larvae, and these are often enabled to live in special environments, unlike those inhabited by the ancestors or by the adults, through possession of peculiar larval modifications. The majority of insects have such modified larval stages, and many of them depart so far from the phylogenetic path of development that they are able to metamorphose into the adult only through the interpolation into the life history of a pupal stage, during which the entire internal and external organization of the larva is rapidly reworked into that characteristic of the adult. Modifications of the developmental stages, such as these, may be thought of as things added to or lost from the original ontogeny, often so altering and distorting the pattern of development that the evidences of recapitulation become difficult to detect.

THE EVIDENCE FROM COMPARATIVE PHYSIOLOGY

Basic similarities in the physiological properties and functions of organisms offer the same testimony of blood relationship as do their structural resemblances. Thus the well-nigh universal presence of chlorophyll in plants is interpreted as evidence that plants are more closely related to each other than they are to animals, in which this substance does not occur. Similarly, the presence of the substance hemoglobin in special blood cells is characteristic of vertebrate animals and indicates that they are more closely related to each other than they are to other animals that lack this substance. The scattered instances in which hemoglobin is found outside the vertebrate group serve only to emphasize the common heredity of the vertebrates, since in these other animals (certain annelid worms and the aquatic larvae of a small fly, Chironomus) the hemoglobin is diffused in the blood plasma instead of being within the blood cells and is different in chemical constitution from any vertebrate hemoglobin.

Degrees of Relationship May Be Determined by Chemical Tests. Since each kind of zygote is destined to develop into one particular kind of organism and no other, it is evident that the differences between any two organisms are inherent in their protoplasms. Basically, such diversities are doubtless the result of differences in the total genotype, which may manifest themselves both as dissimilarities in cell and body organization and as differences in the nature of the chemical products of cell activity. The protoplasm and cell products of closely related species should be very much alike; those of only remotely allied organisms quite unlike, and it should be possible to detect degrees of relationship by chemical means. This has actually been accomplished by several methods, the most delicate tests being the *precipitin reactions*, based on a peculiar property of blood.

If any foreign protein (white of egg, snake venom, blood proteins from another species, or the bodies of bacteria, for example) is introduced into the blood stream of an animal, this protein acts as a poison; in sufficient concentration, it will cause death, but the amount necessary to kill the animal varies with the protein. Injection of lesser amounts than the lethal dose causes the blood to produce certain antagonistic or protective substances called *antibodies*, which in some manner neutralize or offset the injurious effects of the foreign protein. Classified according to the effects that they produce,[1] there are several sorts of antibodies; some, the *agglutinins*, cause clumping or gluing together of the substances on which they act, which are for the most part bacterial cells; others, the *cytolysins*, dissolve the cells whose presence caused their formation; a third class, the *precipitins*, form a precipitate with foreign proteins. It is the last class of antibodies that is used in testing blood for degrees of chemical relationship. Like other antibodies, the precipitins will react fully only with the particular kind of protein (known as the *antigen*) that caused their formation. Their specificity is not, however, absolute; a milder reaction occurs with related proteins, and the degree of the reaction corresponds very closely to the degree of chemical similarity between the protein tested and the original antigen.

In making precipitin tests, blood serum from an animal (man, for example) is injected in repeated small doses into an experimental animal. (Rabbits have been most commonly used for this purpose.) The blood of the rabbit forms antibodies, including precipitins, in reaction to the antigenic proteins present in the human serum. When the blood of the rabbit has been fully sensitized to the proteins present in human serum, the animal is killed, its blood is drawn off, allowed to clot, and the serum thus obtained is filtered and preserved. This "antihuman" serum is now a chemical reagent by means of which there can be made an exceedingly delicate test for human blood, not only when the latter is fresh but also when it is in the form of dried blood stains or even when it is putrid. This test has been extensively used in criminological practice. The blood to be tested is prepared as a weak solution, into which a few drops of the "anti-human" rabbit serum are introduced. If the suspected blood is human, a dense white precipitate at once appears. If, on the other hand, the blood is that of some other vertebrate, there is no immediate reaction, though a smaller amount of precipitation may eventually occur. If the substances tested are not blood or are blood of an animal other than a vertebrate, no reaction takes place.

A generalized statement of the method of making precipitin tests will aid in showing how these are used in determining relationships among organisms. An animal X (generally a vertebrate) is systematically poisoned by having injected into it the blood of another animal *A*. (The juice of some plant or any other protein-containing substance may be substituted for *A*, depending on the use to be made of the test.) This results in the formation in the blood of *X* of specific antibodies against the particular proteins present in the blood of *A*. When the blood of *X* has thus been fully sensitized, a small quantity of its serum, introduced into a solution containing the serum of *A*, will cause rapid formation of a maximum amount of precipitate. Introduced into solutions containing the sera of animals *B*, *C*, *D*, etc., lesser amounts of precipitation will take place, and the time required for the reaction is increased. The rate and amount of the reaction are proportional to the degree of chemical similarity between the proteins present in the bloods of animals *B*, *C*, *D*, etc., and those of animal *A*.

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[1] This is the only way by which we can recognize and classify them; none of them has ever been isolated, and their chemical nature remains unknown.

In the early part of this century, two workers, Nuttall and Graham-Smith, made thousands of such precipitin tests and thus determined the degree of chemical relationship among the bloods of a great many animals. They found that, whereas a prompt and strong reaction was usually obtained only from the blood of the species used for making the antigen (animal *A*), a weaker and slower reaction occurred with the bloods of other species that, from morphological and other evidence, appeared to be nearly related to *A*. By using strong solutions and allowing more time for the reaction, quite distant relationships could be determined. In almost every instance, their results merely served to confirm the conclusions concerning relationships that had previously been reached by other methods. Wherever the evidence from comparative anatomy was clear, this new chemical evidence was in general agreement with it. The more important conclusions reached by Nuttall and Graham-Smith may be summarized as follows:

1. By using sufficiently strong solutions and allowing enough time for the reaction, a chemical relationship can be demonstrated between the bloods of all mammals.

2. Within the group of the Primates, the closest blood relationship to man is found in the great apes; the relationship of human blood to that of the other primates is somewhat less close in the case of the Old World monkeys and diminishes progressively through the New World monkeys and the marmosets to a minimum in the case of the lemurs. Nuttall calls attention to the parallelism between these results and the conclusions arrived at from the study of the macula lutea of the eye, which is present in the higher anthropoids but tends to disappear as we descend in the scale of the New World monkeys and is absent in the lemurs.

3. The bloods of the carnivorous mammals are more nearly related to each other than any of them are to the bloods of other mammals, and

the greatest similarity occurs in the bloods of forms that seem closely related on the basis of structure. The bloods of seals and sea lions (aquatic carnivores) are related more closely to those of dogs, cats, and bears than to those of other mammals.

4. Close chemical relationship exists between the bloods of members of the pig family. Anti-pig serum reacts moderately with the bloods of ruminants and camels and moderately to slightly with that of whales. The bloods of llama and camel are related, and the relationship among deer, antelopes, sheep, goats, and oxen is close.

5. The relationships of the whales and porpoises have been hard to determine from their morphology, which is so highly modified in relation to their aquatic life that resemblances to other mammals are few. The blood of whales gives a faint to moderate reaction with anti-pig serum; the bloods of pigs and other ruminants give slight reactions with anti-whale serum; and there is no evidence of as close chemical relationship of the blood of whales with any other group of mammals. Here is one instance in which the indications from blood tests are at variance with those of comparative anatomy and paleontology, which suggest a derivation of the whales and porpoises from primitive carnivores of the extinct group known as creodonts; from the latter all modern carnivores are believed descended.

6. The bloods of all marsupial animals except the so-called "Tasmanian wolf" were found to show a strong degree of relationship.

7. The reptiles fall into two blood-relationship groups—the turtles, crocodiles, and alligators in one and the lizards and snakes in the other.

8. The birds show closer blood relationship to the turtle-crocodile group than to the lizard-snake group—a result in conformity with paleontological evidence. The blood proteins of all birds are evidently similar, since a strong reaction was obtained with the bloods of 792 species using anti-chicken serum and with 649 species using anti-ostrich serum. This uniformity in blood constitution among birds is in sharp contrast with the diversity among mammals.

9. The horseshoe crab, or king crab, Limulus, is shown by morphological, embryological, and paleontological evidence to be more closely allied to the arachnids (spiders, scorpions, etc.) than to the crustaceans (crabs, lobsters, etc.), which it superficially resembles. It is exceptionally interesting to find that the blood test supports the conclusions arrived at from other evidence.

The degree of chemical similarity between the hemoglobins of various animals has also been determined from a study of their crystalline structure. Reichert and Brown have demonstrated by this different biochemical method that, in general, the more nearly animals are related by morphological and embryological evidence the more nearly similar are their bloods in a chemical sense. Within a genus of animals, they found that the hemoglobins all belong to the same crystallographic system and usually to the same restricted group of that system, and that at the same time those of each species possessed a constant individuality. This signifies that, although each species has its own hemoglobin, those of related species correspond in fundamental chemical constitution.

It must not be thought that there is any exact ratio between the degrees of chemical relationship indicated by the tests described above and those shown by morphological, embryological, and paleontological evidence. Any such assumption would require us to believe that an ostrich and a parrot, for example, are much more closely related to one another than a wolf and a hyena, which would be absurd in the light of other evidence. We can only suppose that in some groups, such as the birds, the blood has changed and differentiated much more slowly than in other groups, such as the mammals.

Methods similar in principle to those described above have recently been applied to the study of relationships among plants and have given results comparable to those obtained among animals. It seems amply demonstrated that the protoplasms and cell products of morphologically similar plant and animal species are chemically more alike than they are like those of morphologically dissimilar species. The only satisfactory explanation that has been offered for these chemical homologies is that they have come about through descent with modification from common ancestors.

The evidence of evolution that is presented by morphology, embryology, and physiology is admittedly indirect. The existence of homologous resemblances, of parallelisms in embryonic development, and of graded degrees of chemical relationship between organisms does not in itself prove that evolution has occurred. The real strength of the evidence furnished by these fields lies in its abundance and consistency. We are faced by a host of striking and otherwise inexplicable parallelisms in the basic details of the structure, development, and functioning of many diverse organisms. These parallelisms are real; we encounter them on every hand; and they may be regarded as evidence of evolution, because under the touch of that theory they fall into place like the pieces of a picture puzzle, making sense where before they were meaningless.

It is impossible to resist the conclusion that homologies are the result of descent with modification from a common ancestral stock, especially when the data from comparative embryology present such an abundance of corroborative evidence. In many instances, indeed, the parallel data from these fields provide a clue to the actual lines of descent and make it possible to postulate definite ancestral types for many existing stocks. (Such predictions have frequently been confirmed in striking fashion by the subsequent discovery of fossil organisms showing the postulated characteristics.) The existence of vestigial organs is likewise inexplicable except on the hypothesis that they are modified remnants of organs that were present as functional structures in an ancestral species. The demonstrated existence of chemical and other physiological similarities among apparently related species can scarcely be a matter of chance, and is a logical necessity if the organisms showing such similarities are parts of a continuing "line" of protoplasm.

If only a few instances of homology and graded resemblances among organisms were known, it might be justifiable to invoke coincidence to explain them; but they are legion. The cumulative weight of the indirect evidence is overwhelming, and perhaps most convincing of all is the way in which the facts discovered in one field dovetail with and support the evidence derived from all other fields.

CHAPTER XXVI

The Evolutionary Significance of Taxonomy, Ecology, and Biogeography

BESIDES the evidence from morphology, physiology, and embryology discussed in the preceding chapter, there is another way in which organisms testify to the reality of evolution. If species have actually arisen from common ancestral stocks, then we should expect them to show graded degrees of resemblance that would appear in their classification. This should manifest itself in a hierarchy of categories that would, in fact, be an expression of the various degrees of blood relationship between species. Such a system of classification should be internally consistent; and we should not find organisms showing a jumble of characteristics that cut across the lines of the major categories—combining, for instance, coelenterate with arthropod and vertebrate features in the same animal. Furthermore, species that have been derived from common ancestors by an orderly evolutionary process ought to exhibit definite and consistent patterns in their geographic and environmental relations.

The fact that organisms do overwhelmingly conform to such expectations is not, perhaps, conclusive evidence that evolution has occurred, but it is at least consistent with the evolutionary concept, and is otherwise unexplained. If, in the discussion that follows, we assume the reality of evolution, we shall see how this illuminates and gives meaning to the facts of classification, adaptation to environment, and geographic distribution. At the same time, we shall examine some of the procedures and concepts of taxonomy and biogeography that furnish a useful background for our coming survey of the geological history of life.

TAXONOMY AND EVOLUTION

The classification and naming of organisms, or the science of *taxonomy*, was originally simply a matter of convenience and necessity; and one of its main functions has been and continues to be the cataloguing and naming of animals and plants. Our survey of the multiplicity and variety of living things has shown how necessary it is that there should be one universally accepted name for each species, if biologists are to understand one anothers' work. From this standpoint, taxonomy is concerned with *distinguishing* among organisms and hence is concerned with their differences. Since the establishment of the principle of evolution, however, taxonomy has become equally concerned with the discovery and expression of *relationships,* in a system of classification that assumes that degrees of homologous resemblance correspond with degrees of relationship among organisms.

Species and Genus. When, in everyday language, we speak of various "kinds" of animals, this term is used without any very precise meaning. Sometimes it refers to groups of very similar individuals, such as cows or sheep, which breed together and form a population in a very restricted and definite sense. At other times, "kind" is used more loosely to include much broader and less definite groups of organisms, as when we refer to snakes or fishes, which obviously are of more than one sort. In biology, it is necessary to distinguish among the different sorts of "kinds"—to establish more inclusive and less inclusive categories for organisms.

The term *species* (spelled alike in the singular and plural) is applied to groups of closely similar individuals, such as men, or English sparrows, which, in general, *are alike in most morphological and physiological characters, reproduce among themselves, and have a common ancestry.*

Actually, it is extremely difficult to give a good definition of species that will apply throughout the animal and plant kingdoms, as will be appreciated when one remembers the alternation of sporophyte and gametophyte generations in ferns, the various phases in the life history of the liver fluke, the regional differences that exist within widespread interbreeding animal or plant populations, and the extremes of variation that have been produced by selective breeding in such species as the dog. Nevertheless, even if the species is hard to define, it is usually possible to tell definitely what is and what is not a species in any particular group, and a few examples will help to make clear the concept.

In the southeastern United States, there occur two kinds of squirrels, the gray squirrel and the fox squirrel. Each of these is a species; but they are both squirrels; hence "squirrel" is a larger category that includes both species. There is also found in this same region another somewhat similar animal, the flying squirrel, which is also a species. However, it is sufficiently different from the other two so that we do not include it in the "squirrel" category but in a distinct one, the "flying squirrel." Again, among the birds of this region are two sorts of crows, the fish crow and the common crow, both of which are species but which show so many similarities that we group them together as "crows." The larger categories in which we group similar species are called *genera* (singular, *genus*). The fox squirrel and gray squirrel belong to one genus, the flying squirrel to another, the two crows to a third.

The Naming of Organisms. It is sometimes asked why it is necessary to give scientific names to animals and plants. The reasons are two: (1) The vast majority of organisms are nameless and unkown until they are described by biologists. (2) Common names are neither precise nor universally understood. Even within the limits of the United States, the same species may bear a dozen or more names in different regions, or a single name may be applied to quite unrelated species. Thus, in the North and West, "gopher" means a small burrowing mammal, whereas in Florida and other parts of the South, it designates a tortoise. On the other hand, each species of organism has one and only one valid technical or "scientific" name, which is the same for scientists of all countries and all times.[1]

Each species has a name consisting of two Latin words, or words in Latin form—the first the name of the *genus* to which it belongs, the second that of the *particular species* of that genus.[2] To make clear how this method operates, we may suppose that we are classifying human individuals by name. The Smiths would be one genus, and the individuals (species) of that genus would be Smith, John; Smith, Richard; Smith, Louis; etc. Similarly, the name of the "squirrel" genus is Sciurus; of the "flying-squirrel" genus, Glaucomys; of the "crow" genus, Corvus. The names of the species mentioned above are *Sciurus niger* (squirrel, black = fox squirrel); *Sciurus carolinensis* (squirrel, living in the Carolinas = gray squirrel); *Glaucomys volans* (gray mouse, that flies = flying squirrel); *Corvus ossifragus* (crow, that breaks bones = fish crow); *Corvus brachyrhynchus* (crow, with a short snout = common crow). The use of Latin for scientific names is a heritage from the days when Latin was the language of science; but Latin has the advantage of being widely understood and of being not subject to change, since it is no longer a living tongue.

The Taxonomic Categories. Starting with the *species* as the basic unit in classification, we have seen that several or many similar, and presumably related, species are assembled to form a *genus*, which is a "kind" or category higher and more inclusive than the species. In similar fashion, several or many related genera may be grouped to form the next higher unit, the *family;* families may be grouped into *orders*, orders into *classes*, and classes into *phyla*. The phylum is the largest division of the *kingdom*, and the plant and animal kingdoms together include all forms of life. Every species is thus simultaneously a member of a genus a family, an order, a class, a phylum, and a kingdom.

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[1] This is true in theory and increasingly in practice. There are, however, many difficulties involving synonymy and the rules governing nomenclature.

[2] This two-name, or *binomial*, system of nomenclature was the invention of a great Swedish naturalist, Linnaeus, and is regarded as beginning with the publication of his *Species plantarum*, in 1753, for botanical nomenclature, and of the tenth edition of his *Systema naturae*, in 1758, for zoological nomenclature. Because of the great numbers of scientists who have occasion to name organisms, it has been necessary to draw up detailed *International Codes of Botanical and Zoological Nomenclature* to govern the making of names and their use. The most important rule is that which states *the oldest name is the only true one.* Another rule is that *the name of the genus must be capitalized*, whereas the second or *specific name* generally—always, in zoology—*begins with a small letter.*

Sometimes these categories are not sufficiently numerous to show all the important groupings that can be recognized among the species of a given category. In this event, additional categories are inserted and are designated as *subspecies,* or *sub-* or *super-*orders, families, etc. The principal categories are illustrated in the accompanying diagram showing the classification of the five species mentioned above.

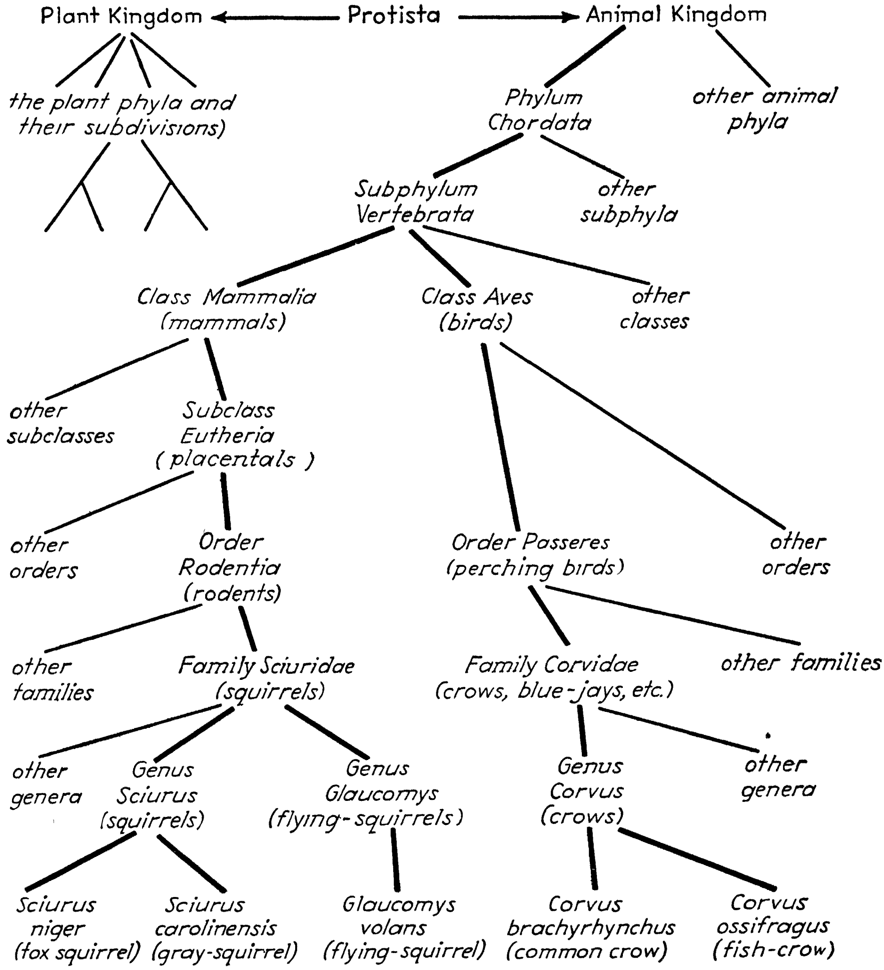
Plant Kingdom
Protista
Animal Kingdom
the plant phyla and their subdivisions)
Phylum Chordata
other animal phyla
Subphylum Vertebrata
other subphyla
Class Mammalia (mammals)
Class Aves (birds)
other classes
other subclasses
Subclass Eutheria (placentals)
other orders
Order Rodentia (rodents)
Order Passeres (perching birds)
other orders
other families
Family Sciuridae (squirrels)
Family Corvidae (crows, blue-jays, etc.)
other families
other genera
Genus Sciurus (squirrels)
Genus Glaucomys (flying-squirrels)
Genus Corvus (crows)
other genera
Sciurus niger (fox squirrel)
Sciurus carolinensis (gray-squirrel)
Glaucomys volans (flying-squirrel)
Corvus brachyrhynchus (common crow)
Corvus ossifragus (fish-crow)

FIG. 116. *Diagram showing the principal taxonomic categories.*

Taxonomy as an Expression of Relationships. If the naming and cataloging of species were the main object of classification, any convenient artificial arrangement would suffice. Such taxonomy is merely a method—no more a science than a card-filing system is. But modern taxonomy has the status of a science, because it is an attempt to discover and express phylogenetic[1] relationships among organisms—an attempt that would be meaningless except for the evolutionary concept. To attain this end, use is made of data from all fields of biology that can throw light on relationships. Morphological data, being the easiest to obtain, are of necessity the foundation for a large part of the system, but these are supplemented wherever possible by the findings of embryology, physiology, paleontology, biogeography, and genetics.

The assignment of organisms to categories is not arbitrary; it is based upon the fact that the different species possess more or less numerous characteristics in common and can be grouped into restricted or inclusive categories according to degree of relationship as determined by homologous resemblances and other evidences. To illustrate this point, we may turn once again to the squirrels.

The squirrels and flying squirrels share with the woodchucks, prairie dogs, and chipmunks numerous features that indicate relationship. The species and species groups (genera) of these animals are assembled into a larger unit, the family Sciuridae, as an expression of this relationship. All members of the Sciuridae have long, chisel-shaped incisor teeth, fitted for gnawing, and lack canine teeth; but these characters and certain others that accompany them are found to extend over a larger assemblage of animals than the squirrels and their allies. They also occur in the families that include the rats and mice, the beavers, the porcupines, and the pocket gophers (the burrowing mammals that are called *salamanders* in the southeastern states). Because of this and other facts, all these animals are evidently related, though somewhat more distantly than are the species belonging to any one family. We group all these families into a large unit, the order Rodentia, or *gnawing mammals*. In similar fashion, we find that all the members of a number of orders, including the Rodentia, the hoofed mammals, or Ungulata, the flesh-eating mammals, or Carnivora, and the Primates agree in having a placenta and in other features; they are grouped together into the subclass Eutheria, or *placental mammals*, in recognition of the fact that they are related by common descent, though somewhat distantly. All the other groupings of the species of the animal and plant kingdoms are based on the same principle. Scientists do not make these groups but merely try to recognize their existence and give them appropriate names when they have been found.

The evidence of evolution that is contributed by taxonomy is admittedly open to the criticism of "arguing in a circle." However, the fact that a system of classification based upon "degrees of relationship" is capable of accomplishing a graduated and detailed grouping of all organisms is in itself testimony to the consistency and practicality of the evolutionary concept.

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[1] Phylogeny (Greek, *phylon*, "race," and *genesis*, "origin, descent") refers to racial origins and development.

ECOLOGY AND EVOLUTION

When we examine the relationships between organisms and their environments with the concept of evolution in mind, whole classes of facts take on significance that otherwise would be mere unexplained peculiarities of individual species. Thus we find, among the species belonging to a single family or order, a wide variety of ways of living and corresponding variety in the types of situations occupied. Among the members of the squirrel family, all clearly related by morphological evidence, some are arboreal, others terrestrial, and still others burrowers in the soil. Yet they are all built on a common structural pattern that is modified in relation to the mode of life of each species. Occupation of different habitats by the modified descendants of a common ancestral stock affords an acceptable explanation of these phenomena.

The *adaptation* of organisms to particular modes of life has two aspects. On the one hand, there is the great perfection of many adaptive structures and behaviors, perhaps reaching its extreme in some of the varied host-parasite and mutual-benefit types of relations between different species. On the other hand, we must note the rather frequent cases in which species are imperfectly adjusted to their environments, or fail to show adaptive features that would seem to be desirable. Both of these aspects become understandable if we regard adaptations as resulting from evolutionary modification of something which the organism already possessed. Sometimes a structure or process or behavior was present that furnished material from which a new adaptive feature of changed function could arise; but in other instances the organism possessed nothing that would serve as a starting point for such a development. Furthermore, if evolutionary modification of an organism fails to keep pace with changes in the environment, the organism may be imperfectly adapted in some respects, or even exhibit useless or harmful characteristics.

To illustrate the relation between evolution and adaptation, we may turn once more to the squirrel family, the Sciuridae. As part of their basic equipment, inherited from common ancestors, all members of this family have claws and tails. In the squirrels proper, the claws have become sharp spikes which enable the animal to cling to tree-trunks or to move about sure-footedly on branches, digging the points into the bark much as a linesman uses his climbing tools. The tail has also been modified into a graceful balancing organ. The flying squirrels show the same changes, but in addition the skin of the sides of the body has become a loose flap which can be tightened by extending the legs, and the tail hair grows out in a horizontal plane, so that the body as a whole can be used for gliding. The prairie-dogs have become burrowers in the soil; their claws are modified into strong digging tools, and the useless tail has been reduced to a mere stub. In none of these related types are the special adaptations really new structures but only modifications of the inherited features common to all members of the family. The phenomenon here illustrated by the squirrels—a spreading out of the descendants of a single original stock into more and more numerous and diverse types of environment, with concomitant adaptive changes—has been called *adaptive radiation.* We shall encounter additional examples of this phenomenon in our survey of the geological history of organisms, particularly in the account of the mammals.

From the standpoint of ecology, then, it appears that the evolutionary principle affords a satisfying explanation of the occurrence of adaptation and adaptive radiation, as well as of the imperfection or absence of adaptive modifications in many instances.

BIOGEOGRAPHY AND EVOLUTION

Everyone knows that the species of animals and plants are not universally distributed; lions do not occur in North America nor snakes in Ireland. It is obvious that the failure of an organism to occur in a given region may result from its ecological requirements. We should not expect to find alligators in deserts or sagebrush in marshy regions; and the same principle applies in many instances that are not so self-evident. Indeed, every species of animal and plant has a particular set of requirements that limit the environments in which it can live.

On the other hand, scarcely any species is found in all parts of the world where conditions are suitable for its existence. There were no rabbits in Australia until they were brought there by European settlers; but this was not because of any unfavorable factor in the Australian environments, for as soon as rabbits were introduced, they multiplied until they became a pest. It is clear, then, that other factors than ecological ones must play an important part in determining the present geographic ranges of species, and it is these other factors to which our attention is now particularly directed.

The geographic distribution of organisms is not haphazard but follows a definite pattern. That portion of the earth inhabited by a particular species constitutes its *range.* Size of range varies tremendously, from a few square miles in the case of some species to all the continents in the case of man. Closely similar species seldom occupy identical or widely overlapping ranges; on the other hand, their ranges are not often widely separated; instead, they are generally adjacent and are commonly separated by some sort of a barrier that prevents free intermingling of the two species populations. Entire groups may be absent from regions that have been long isolated from other parts of the world, and the faunas of such regions tend to be made up largely of species peculiar to them.

Such facts as these are explainable only as the results of organic evolution. Not only do they take on meaning in the light of this concept but the findings of biogeography also aid in understanding the process of species formation, as will be discussed later. The similarities among species that occupy adjacent ranges are natural if they are both descendants from what was once a single species, which have become different in the two areas because they have been isolated in some manner and have evolved along divergent lines. The occurrence of peculiar species in long-isolated regions may, on the evolutionary principle, be explained in part as survival of early types that elsewhere have been replaced by more modern ones, in part as the result of evolutionary modification of species that, as waifs, have accidentally reached the area.

The remainder of this chapter will be devoted to a more detailed consideration of the principles that govern the distribution of organisms, and in this discussion the truth of the evolutionary principle will be taken for granted.

Factors That Determine the Geographic Distribution of Species. The range of any given species is the result of a unique combination of requirements and events, but analysis of the factors involved shows that they always include the following:

I. Ecological factors
   A. The constitution of the organisms, including its ecological requirements and the changes in these that occur as a result of evolution.
   B. The nature and distribution of the present physical and biotic environments in which it can live.
II. Spatial and related factors.
   A. The place where the species originated and from which it has spread.
   B. The means of dispersal available to the species and the spatial distribution of barriers to and highways for its spread.
III. Historical factors.
   A The time of origin of the species, as a result of which it has been subject to the effects of a longer or shorter sequence of
   B. Changes in
      1. The physical environment, as regards both ecological conditions within the range and the spatial relations of barriers and highways; and
      2. The biotic environment, as modified by evolution and migration.

The present geographic and ecological distribution of any species is the resultant of the operation of all these factors throughout the period of its existence. Insofar as differences in the geographic location of species and in the extent and form of their ranges do not result directly from the distribution of their habitats, they are determined by the spatial and historical factors listed above.

Place of Origin. A fundamental working hypothesis in biogeography, and one that is borne out by all the available evidence, is that each species of animal and plant has originated in a single place and only once. The place where the species arose, although it is often called the *center of origin*, is not to be thought of as a point in space but as an *area* that comprised a part of the range of the ancestral stock. Thus the center of origin of one species may have been the southeastern coastal plain of the United States; of another, the Ozark highlands; and of a third, the Gobi desert. By extension, we may speak of the center of origin of a genus or family, meaning the range of the ancestral species from which the modern representatives of the group have descended.

The place of origin of most species is included within their present geographic range, but this is not invariably the case. Numerous species are known which formerly had a much wider range but which now are restricted in occurrence; some of these doubtless originated in an area where they no longer occur. The place where a species came into existence obviously has an important bearing on its present geographic location; a species that arose in North America is likely to be there now (unless it has become extinct) and is much less likely to be found in Africa.

It is sometimes asked why, if species change through mutation, a new species might not arise independently in two or more widely separated areas through the occurrence of the same mutation in different parts of the range of a widespread parent species. Theoretically, this is possible, and it may sometimes have occurred; but the chances are overwhelmingly against its happening For one thing, most species do not differ from their nearest relatives by single gene differences but by numerous ones. Instead of arising as a result of single mutations, species are believed normally to develop as a result of the slow accumulation of numerous gene changes in an isolated part of a species population. Furthermore, each region has its own set of environmental factors, to which the new form must be adjusted if it is to survive. The chance is negligible that many identical gene changes will occur independently in two regions with sufficiently similar environments to ensure the survival of the new forms.

Dispersal in Relation to Barriers and Highways. Pressure of population makes every successful species tend to spread out over more and more territory—to extend its range. The gradual expansion of the ranges of animals and plants that results from their normal activities is known as *spreading*. In the case of most animals, spreading is *active*, being brought about by random wanderings in search of food, mates, and shelter and by the ordinary means of locomotion of the species. In the case of plants and some groups of animals, the organism is fixed in position or has locomotor powers too small to bring about significant changes in location. In these cases, spreading is *passive* and results from the transportation, by wind, currents of water, or animals, of seeds, spores, eggs, resting stages of small aquatic organisms, or even the organisms themselves. Many or most of the species that depend upon passive spreading have some stage in the life history especially adapted for transportation; examples are winged seeds, burrs that stick to the hairy coats of mammals, and the minute free-swimming larvae of many sessile marine organisms.

In some instances, there is a definite behavior directed primarily toward dispersal, and to such instances we may apply the term *migration*. As examples, there may be cited the *sporadic* outpourings of the lemming (a small mouselike mammal) from its home in the Scandinavian uplands, or the *periodic* spring and fall migrations of many birds. Migration is far less likely to bring about permanent extensions of range than is spreading, though it may occasionally have this result. Its causes and effects are complicated and are only partially understood.

Lastly, both plants and animals may be transported accidentally by such agencies as hurricanes, floating rafts of vegetation, or the feet of wading birds in the case of small aquatic organisms. With the advent of commerce, man has become the chief agent of accidental dispersal and has been the means of carrying large numbers of species to regions distant from their original homes.

Barriers. In the instance of very recently developed species, not all the available territory may yet have been occupied, and the species may be seen to extend its range from year to year. Thus, among certain newly originated species of land snails inhabiting Tahiti and Moorea (islands in the South Pacific), studies by Garrett, in 1861–1884, and again by Crampton, in 1907–1923, showed that some of the species were steadily increasing their ranges. The same phenomenon of spread over unoccupied territory is more strikingly exemplified in the rapid dispersal over North America of such introduced species as the English sparrow and the starling, not to mention the dozens of introduced insect pests.

Sooner or later, however, the expanding population encounters some obstacle to further progress. It may be an obvious physical barrier—a high mountain range, a great river, or the sea (for a land animal); or land (for an aquatic species). However, most species do not succeed in spreading until their ranges are limited on all sides by such barriers. Far more often, the range is bounded through much of its extent by zones wherein one or more ecological factors—humidity, temperature, food supply, shelter, soil, etc.—change to a point beyond the limits of toleration of the species. Here there is no physical impediment to further spread, but an inability of the species to maintain itself permanently in the region beyond. Establishment in a new habitat is called ecesis, and hence barriers of this sort are known as *ecesic barriers*, or barriers to establishment.

Highways. Most species are soon hemmed in by barriers that determine the extent of the range. In some instances, however, there may be a gap in the barriers at some point, leaving a relatively restricted highway along which the species can spread, perhaps to enter another region suitable for its existence. Thus, many of the species characteristic of the cool, forested regions of southern Canada are in most places limited southward by a temperature barrier but find a southward-leading highway in the Rocky Mountains, along which they have extended as far as the higher mountains and plateaus of New Mexico and Arizona.

Again, at various times during the Cenozoic,[1] there has been a temporary land connection between Siberia and Alaska, across the narrow Bering Straits, which formed a highway for interchange of species between the Old and New Worlds.

Historical Factors in Distribution. In a geological sense, highways and barriers, both physical and ecesic, are impermanent. The longer a species or group of organisms has been in existence the more chances it has therefore had to spread away from its place of origin, through disappearance of old barriers and formation of new highways. At the same time, the appearance of new barriers and elimination of old highways may have brought about discontinuity between the populations descended from the ancestral stock. Interchange of new gene characters appearing in these isolated populations is thereby prevented, and the populations tend to diverge along different evolutionary paths.

Entry of species along newly formed highways into hitherto inaccessible areas results in changes in the biotic environment—new competition between species adapted to similar modes of life, new enemies and new food supplies, new parasites and diseases. The result of such invasions is generally the extinction of some species and certainly a readjustment of all biotic relations within the invaded area.

Although we may thus generalize as to the *types* of effects that result from the operation of historical factors, each species and group of organisms has had a particular and, in its details, a unique history, dependent upon the historical sequence of events in relation to which it has developed and in which its own potentialities for distribution, evolutionary modification, and successful competition have played a part. The following examples illustrate some of the ways in which particular groups of organisms may be influenced by the operation of historical factors.

Discontinuous Distribution and Extinction. True alligators are today confined to the southeastern United States and to the Yang-tse River in China. Paleontological evidence shows that they had a wide and continuous distribution in the Northern Hemisphere during the early Cenozoic; but environmental changes associated with elevation of the western part of North America, the cooling and drying of the climate during the Pliocene, and the Pleistocene glaciations resulted in their extinction over most of their former range. The Chinese and American forms have become sufficiently different to be regarded as distinct species.[2]

During the Pleistocene, many species of animals and plants spread southward in the United States with cooling of the climate and advance of the glaciers. When the ice sheets receded, the bulk of the populations of these species again shifted northward; but here and there, in isolated pockets where conditions were sufficiently cool and moist, relict colonies were left south of the main body of the range. Such relict biotas occur in several places in western Florida (in the region from Tallahassee to Marianna, and especially in the Torreya ravines along the Apalachicola River). In these isolated spots, northern types of animals and plants occur, cut off from the rest of their species; some of them already show slight differences from their northern relatives.

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[1] The geological periods mentioned in the following account are shown in the time scale given facing p. 348 and are discussed in Chaps. XXVIII to XXX.

[2] It is probable that specific differentiation had already occurred, or at least begun, before the ranges of these two species became discontinuous.

Isolation from Severe Competition. The marsupials were the dominant mammals of the late Mesozoic and spread to most parts of the world. Prior to the Cretaceous, a land bridge connected Australia with southeastern Asia, and over this highway the marsupials spread into Australia. The connection was broken during the Cretaceous, before the placental mammals had an opportunity to reach Australia. Elsewhere in the world, the marsupials were supplanted by the more successful placentals; but in Australia, they constituted the entire mammalian fauna and were protected from such competition. Under these circumstances, they underwent *adaptive radiation*, *i.e.*, they developed a great variety of types adapted to nearly all the modes of life available to mammals. Many of these marsupial types are analogous to placental types that evolved in the remaining continents. In other words, adaptive radiation within the marsupial stock was accompanied by *convergence* toward corresponding types produced by adaptive radiation among the placentals.

On oceanic islands similar phenomena are observable. Thus on many such islands large, flightless, defenseless species of birds, such as the dodo, solitaire, and relatively gigantic Mauritian parrot, were able to develop in the absence of predaceous enemies. They fell easy prey to man and were exterminated soon after the discovery of their island homes. A relatively small number of insect species have been able to reach the isolated Pacific islands by accidental dispersal prior to the days of commerce, but once introduced they gave rise to many related forms, unhindered by competition from other species. As a result the insect fauna of these islands has a peculiarly unbalanced composition, many groups being absent, and others being represented by a wealth of more or less closely related endemic species. The same phenomenon is strikingly shown in other groups, such as the land snails of the Hawaiian and Marquesas islands, in which speciation and adaptive radiation have multiplied the species of a few original stocks to an amazing extent, furnishing classical examples for study of the speciation process.

Effects of Entry of Better Adapted Competitors. During the Paleocene and Eocene, North America was inhabited by numerous groups of archaic, small-brained placental mammals, most of which became extinct at or before the close of the Eocene. It is noteworthy that this extinction coincided with an incursion of modernized types of [illegible] mammals from the Old World.

The causes of extinction of the archaic forms were probably complex, but it can scarcely be doubted that inability to compete with these bigger brained, more alert newcomers, which were better adapted to the same modes of life, was an important [illegible] factor Turning to comparable instances in the present, we find that [illegible]pial fauna of Australia is steadily diminishing in the face of competi[illegible]ntal mammals introduced by man.

[illegible] *of New Enemies or Parasites.* Instance after instance is known in [illegible]tion of some species by man has resulted in extermination of native species and entire alteration of the biotic relationships of particular regions. The most striking cases are those of island faunas. Introduction of the mongoose into the West Indies resulted in almost complete extermination of the reptile and amphibian faunas of many islands and in great reduction of the bird populations. The tuatara, Sphenodon, which survived in New Zealand because of its isolation, has been exterminated by the introduced rat, except on a few small islands. It cannot be doubted that this sort of thing has happened time and again in the past, when new highways have allowed the entry of hitherto excluded enemies.

The Ranges of Closely Allied Organisms. When we examine the ranges of closely related species (or subspecies), we find that they are not distributed at random but instead conform to certain definite rules. The most evident of these generalizations was first formally stated by David Starr Jordan as follows: "In any group of related organisms, whether species or subspecies, the most closely related will be found, not in the same geographic area, nor in widely separated areas, but in adjacent areas separated by a barrier of some sort." Although this descriptive generalization, known as *Jordan's law,* has had to be amplified as mentioned below, it is found to hold true in the great majority of instances.

Isolation and Speciation. In the closing chapter of Part III, we shall have occasion to recur to the part played by isolation in the formation of new species. At this point, it will suffice to mention that some form of isolation is apparently necessary if a stock is to break up into separate species. The only acceptable explanation for the existence of the distributional relation expressed by Jordan's law is that the two different but related populations that occupy adjacent ranges have arisen from a single ancestral population, and that it is the presence of the barrier that has resulted in their becoming distinct. Such geographic isolation and accompanying speciation is a very common phenomenon; but in recent years, numerous instances have been found of closely related forms occupying the same territory and sometimes even the same habitat. Most of these apparent violations of Jordan's law have not been thoroughly studied. In those that have, it has usually been found that interbreeding between the two forms is prevented or minimized by some form of ecological, physiological, or psychological barrier between them, which takes the place of the geographic barrier in the conventional statement of Jordan's law.

Because this chapter has had a dual purpose, we may conclude it by briefly summarizing the two things that it has tried to accomplish. The first has been an examination of the application of the principle of evolution to taxonomy, the ecological relations of organisms, and their geographic distribution. Here we have seen that whole classes of facts, which are not in themselves evidence of evolution, are nevertheless consistent with this concept and significant only in relation to it. It greatly strengthens our confidence in the actuality of evolution to find that the data from these fields not only affords no conflicting evidence but also takes on new meaning in the light of this principle. The second purpose of the chapter has been to outline briefly the more important facts of classification and biogeography. In doing this, it has been impossible to exclude tacit acceptance of evolution as an established fact, since this principle has become an integral part of the structure of these two subsciences.

CHAPTER XXVII

The Geological Background of Evolution

FROM a consideration of the evidences of evolution furnished by living organisms, we are about to turn to the historic record of evolutionary change that is contained in the rocks. This record, fragmentary though it is, presents us with a surprisingly complete picture of the actual course that evolution has followed. From morphological and physiological data we might feel certain that the horse, zebra, and ass came from some common ancestor, and we might even have predicted many of that ancestor's characteristics, but we could never have reconstructed it bone by bone in minute detail, as has been made possible by finding its remains in the rocks. Nor, probably, should we ever have guessed at the many blind alleys into which life has strayed if we had not had the record of scores of thousands of extinct types that have left no descendants. Not only has paleontology served to confirm and sometimes to correct the general outlines of evolution sketched by the other biological disciplines, but it has also filled them in with rich detail, so that the picture of evolution that we see today is like an ancient mosaic, faulty and defaced in many places, particularly in its older parts, but with its composition and significance clear and many of its finer details still visible.

The present chapter is in the nature of a rather long digression, made necessary at this point in order to make clear how it happened that a record of past life was preserved in the rocks and how it is that we are able to discover, interpret, and reconstruct this record and make of it a connected story. We shall have to review briefly certain aspects of geology, especially those which have to do with the formation of the sedimentary rocks and the various kinds of fossils, the determination of their relative ages, and the reasons for the gaps in the record.

In discussing the history of the evolutionary concept, we mentioned that in the earlier days of science, many geological phenomena were thought to have been produced by great catastrophic disturbances of the past—universal floods, widespread outbursts of volcanic activity, or events referred to merely as "convulsions of nature." Following the enumciation of the hypothesis of uniformitarianism, in 1785, by Hutton, geologists came gradually to accept this as the order of nature and to recognize that even the most impressive features of the earth had for the most part been produced by small forces acting over enormously long periods of time. The modern science of geology is founded upon the principle of uniformitarianism, which embodies the ideas that earth history has been very long, that changes in the earth have in the main been gradual, and that the geological past can be understood only in the light of what we see going on about us. These conclusions apply equally to the history of the earth itself and to that of its inhabitants. It is true that we now recognize that uniformitarianism does not mean that all geologic or evolutionary processes have always gone on at the same rate and under identically the same conditions as at present. There was a time when the earth was molten and no life existed. Even after the reign of uniformity began, in that part of earth history when conditions were more like those of today and animals and plants had come into existence, we know that the rate of geologic and evolutionary change has varied from time to time in more or less cyclic fashion. But with slight modification, the principle of uniformitarianism is today accepted as one of the basic concepts of natural science.

The Rocks of the Earth's Crust. The outer *crust* of the earth is a shell of rock, generally assumed to average about 60 miles in thickness. Distributed about the earth are the continents, great masses of relatively lightweight rock, which float in what is believed to be a continuous layer of much denser, heavier rock. The places where the layer of light rock is thin or absent form the ocean basins. The great bulk of the continental masses is composed of a crystalline rock called *granite*, which, together with other kinds of crystalline rock, was formed by the cooling of molten rock liquids similar to lava. Rocks of this class are called *igneous*, because heat is involved in their origin.

The rocks forming the surfaces of the continents are exposed to the action of air, moisture, changes of temperature, and the influences of plants and animals. The combined effect of these agencies is to cause the rock surfaces to "decay" and disintegrate; this is termed *weathering*. The loose materials thus formed cover the surface; they are blown by the wind, washed down slopes by the rain, and carried off by streams. Where the streams empty into lakes or the sea, the finely divided material (*sediment*) settles to the bottom to form sheets and layers of mud or sand. In the course of time, the earlier formed layers are covered by later ones and, compacted by the weight of overlying material and by chemical changes, harden into solid rock. Such rock, because of its layered structure, may be called *stratified rock;* it is also called *sedimentary rock* in reference to the materials that compose it.

By far the greater parts of the continents are covered by accumulations of sedimentary rocks, spread layer upon layer over the underlying granite. Some of the sheets are relatively local, but many extend over areas of thousands of square miles. Such widespread deposits bear evidence of having been formed in shallow seas that lay upon the interiors of the continents; they represent the mud and sand poured into the seas by the rivers that flowed off the bordering lands. Once they were the muddy and sandy sea bottoms, on which lived marine animals whose shells and bones are imbedded in the sediments, now hardened into rock. In those areas of shallow sea more distant from ancient shores, which the muds consequently seldom reached, the sediments were often composed almost entirely of the limy shells and hard parts of organisms, and became *limestone.*

In many regions the sedimentary layers, or *strata,* are still horizontal, as they were when laid down. But where they are piled up in the deepest accumulations (sometimes several miles thick), they are commonly folded and crumpled into great mountain ranges. This is the result of a sequence of events described below, which has been many times repeated in earth history.

In all the ancient continents, there were some areas that remained land most of the time. The rivers flowing off from these lands deposited the coarser (and bulkier) of their sediments only a little distance offshore. Under the weight of this accumulating sediment, the crust sagged into long narrow troughs bordering the ancient permanent lands, and these troughs were filled with sediment as fast as they deepened. At various periods in earth history, there has been intense and long-continued compression of the crust. At such times, the weakest parts of the crust yielded, and the long, narrow troughs filled with water-soaked sediments were weaker than the masses of crystalline rock on each side.

In successive periods of deformation, first one and then another such trough gave way, crumpling into mountains in such a manner that the sedimentary strata bent into corrugated folds or in places even broke and slid over one another. Where the pressure and the accompanying heat were intense, the nature of the rocks was greatly altered, becoming more or less crystalline, with the formation of new minerals and the obliteration of the original characteristics, including the destruction of all fossils. Thus shales or mud rocks were changed to slates, limestones to marbles, and sandstones to a much denser kind of rock called quartzite. Any rock, whether originally sedimentary or igneous, which has been thus altered by pressure and heat is called a *metamorphic rock.* Where the mountain-making forces acted less vigorously, the sedimentary rocks were thrown into folds without losing their sedimentary characteristics and without destruction of fossils.

Not all sediments have been laid down in the seas, though this is where the greatest accumulations have occurred. They may be deposited in lake basins or in swamps or as river deposits built up like land deltas on the plains at the foot of mountains. Much of our knowledge of the later steps in the evolution of life comes from fossils found in fresh-water and land deposits. From the geological standpoint, however, such sediments are far less important than the marine deposits because of their merely local extent and because they are so much more likely to be destroyed by subsequent erosion.

The Order of the Strata. In an undisturbed series of sedimentary strata, the lowest layers are obviously the oldest, the uppermost the youngest. In regions such as Florida, where the strata lie relatively flat and because of the low elevation streams do not cut deeply into the surface, only the uppermost layers are accessible to study. In such regions, the nature of the deeper strata can be learned only from well borings. On the other hand, in regions where the land has been elevated and the strata left undeformed or only gently tilted or warped, streams have often cut sections through the mass of layers so that their edges are exposed in the valley sides; or erosion has stripped off parts of the surface, so that in crossing a region, one can traverse the beveled edges of the layers.

Each section thus exposed to study constitutes only a small part of the entire rock record, but by correlating the pieces of the story revealed in one area with those preserved in other areas, a fairly complete record of the last quarter or third of earth history has been worked out. Much of this has been accomplished by the use of fossils for correlating distant exposures of rock strata in the following manner. Each stratum is found to have a peculiar assemblage of fossils different from that of other strata. The succession of these fossil faunas and floras can be determined in one region where the rocks lie undisturbed; then the sequence worked out in that region can be used to determine the relative ages of strata in other regions. This method is particularly important in studying the rocks of folded mountains, where the strata may be turned up into steeply tilted or vertical positions or even sometimes folded completely back on themselves, so that locally they may lie in reverse order—younger strata beneath older ones.[1]

The History of the Continents. The results of studies that cannot here be discussed show that the continents and ocean basins have existed since the very beginning of that part of earth history recorded in the rocks. The ocean basins are a little more than brimful of water, so that the edges of the continents are generally covered by shallow seas. Such seas, resting upon the continents, are called *epicontinental seas.*

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[1] Unfortunately, where such disturbance of the strata has been greatest the fossils have been destroyed by metamorphism, and other methods of correlation must be used.

On every continent, a certain cycle of events has repeated itself many times with slight variations. At the *beginning of a typical geologic cycle,* the continent stands high; the epicontinental seas are restricted to the edges; and the high lands are being rapidly eroded by swift-flowing streams that carry their sediments to or over the edges of the continental shelves. As the lands are degraded and the sediments are deposited in the seas, the water level rises and slowly creeps in over the low parts of the land. (Hudson Bay appears to be an example of such an advancing sea.) By the *middle of the cycle,* the lands are worn low, and the interior of the continent is occupied by widespread, shallow interior seas, in which are deposited the sediments from the remaining land areas. With warpings of the continent, the seas slowly fluctuate in form and extent, but they occupy the land for periods of the order of one million to several million years. Finally, toward the *end of the cycle,* a period of readjustment sets in; the continents rise, often with the formation of a mountain range in some part where the sediments were thickest; the seas are spilled off, and the cycle is ready to repeat itself.

This cyclic series of events forms the basis for the subdivision of earth history into periods of time, corresponding to the systems of strata formed during the periods of sea invasion. Each spread of the sea leaves strata of rock on top of those formed during the previous cycles. There are breaks in the series, due to the times when the continent stood high, partly because during these times streams were busy destroying the record of the earlier depositions. These breaks (unconformities) in the rock record also appear to be breaks in the story of life, for the marine forms at least. Life was continually changing, and at each return the seas brought with them a fauna that was different from that of the previous cycle.

On the whole, these cycles have affected all the continents simultaneously, so that the divisions of the rock record in one region hold good for other parts of the world; but there are generally some places where rocks formed during the interval are still accessible. These give us a fragmentary record of what went on in the seas during the period of continental elevation. But at very long intervals, unusually great "revolutions" occurred, in which all the continents stood so high and for so long a time that no record of the interval has been found. During these times erosion also destroyed a vast amount of the earlier records. These great breaks are taken as the dividing points between the major eras of earth history. For reasons pointed out later, they are also times when profound alterations occurred in the world of life, many ancient types becoming extinct, and the evolution of new types being accelerated.

The Concept of Time in Relation to Earth History. The student of science must become accustomed to thinking in terms of several quite different scales of time. Recorded history is only a few thousand years in duration, and in the historical sense, an event of 6,000 years past is very ancient indeed. To the student of human evolution, whose field of inquiry comprises the Pleistocene, or glacial, epoch, an event of 6,000 years ago is quite recent, whereas really ancient events occurred 250,000 or 500,000 years ago. To the geologist, years are of little moment; he deals with a vast period of time in which 6,000 years ago is the same as today and the Pleistocene in its entirety is an insignificant part of the whole. If years are insisted upon, he points out that the oldest known rocks, on the basis of recent physical estimates, are perhaps 1 billion 900 million years old and that, since these do not record the beginning of earth history, a figure of 2 billion 500 million years may be taken as a working hypothesis for the age of the earth. But the geologist and the biologist are much more concerned with the *relative age* and *relative duration* of events, and here they can speak with much greater assurance. Finally, to the astronomer, the whole period covered by the history of the earth is an insignificant fraction of the life of a single star such as the sun.

The Geologic Time Scale. By fitting together the fragments of the rock record preserved in different regions, it has been possible to construct a detailed time scale, in which names are given to the periods of earth history and their sequence is shown. This time scale includes both the known parts of the history and the gaps; the latter probably account for at least as much time as the periods of which there are records. The complete time scale of modern geology is nearly as complicated and contains nearly as many names and events as, for example, a moderately condensed treatise on the history of Europe; but for our purposes, only the most important periods and events are needed. A simplified time scale giving this information is presented herewith. Knowledge of the names of the periods and their sequence is essential to an understanding of the material that is to follow.

Fossils. The life of the past has left a great variety of records, and we can define a fossil as being any trace of prehistoric life. For obvious reasons, fossils are never found in igneous or in strongly metamorphosed rocks. Most fossils have been preserved by burial in sediments, and many sedimentary rocks are literally filled with them. The things most commonly preserved are the hard parts of organisms, such as shells, bones, and teeth. Under exceptional circumstances, even the more

GEOLOGIC TIME SCALE

Eras	Major divisions	Periods and epochs	Events and age in million of years	Plant Life	Animal Life
Cenozoic era 5%	Recent			Decline of woody plants; dominance of herbaceous types	Age of Man
	Quaternary	Pleistocene	Ice ages 1	Great extinction; survival of hardier types	Dawn of social life and industry among men
	Tertiary	Pliocene	Mountain making 25	Decline of forests and spread of grasslands, climates becoming drier and cooler toward close	Man-ape changing into man
		Miocene	35		Climax of mammals
		Oligocene	40	Maximum spread of forests, mild climates. rise of monocotyledons	Rise of anthropoids, last of archaic mammals
		Eocene	60		Spread of placental mammals
		Paleocene	65		Climax of archaic mammals
	Fourth great revolution (Rocky mountain) with little loss of records				
Mesozoic era 8%	Late Mesozoic	Cretaceous	120	First monocotyledons. beginnings of modern forests, widespread forests of oaks, maples, etc.	Last of ammonites. Extinction of dinosaurs, pterosaurs and toothed birds. rise of archaic mammals and modern birds
	Early Mesozoic	Jurassic	150	Increase of the dicotyledons	Rise of toothed birds spread of pterosaurs, spread of primitive mammals climax of ammonites
		Triassic	200	Gymnosperms dominant but gymnosperms and pteridophytes waning	Rise of dinosaurs, pterosaurs and reptilian mammals Extinction of stegocephalians
	Third great revolution (Appalachian) and some loss of records				
Paleozoic era 24%	Late Paleozoic	Permian	Glaciation 210	Spread of the Glossopteris flora from the south, replacing the coal forests	Last of trilobites and paleozoic corals, increase in reptiles, rise of modern insects
	Carboniferous	Pennsylvanian	Coal making 250	The great coal-forests dominated by pteridophytes and gymnosperms	Spread of stegocephalian amphibians and primitive insects
		Mississippian	300	Climax of pteridophytes; gymnosperms rising, first dicotyledonous angiosperms	Spread of ancient sharks climax of sea-lilies
	Middle Paleozoic	Devonian	350	First known forests, rapid increase of pteridophytes and gymnosperms	Rise of amphibians, marine fishes, and goniatites. first spiders.
		Silurian	400	First known land plants	Dominance of marine arachnids, first (wingless) insects (?), spread of paleozoic corals
	Early Paleozoic	Ordovician	475	Marine algae dominant. probably time of origin of the gymnosperms	Rise of fresh-water fishes and corals. spread of molluscs, climax of trilobites
		Cambrian	550	Probably time of first colonization of lands, origin of bryophytes ands pteridophytes	Dominance of trilobites and brachiopods First abundance of fossils
Cryptozoic eon 63%	Second great revolution and consequent loss of records				
	Proterozoic era		1,000	Primitive aquatic plants	Primitive marine invertebrates
	First great revolution and consequent loss of records				
	Archeozoic era		1,900		

perishable soft parts may leave imprints on fine-textured muds or be preserved by petrifaction, by impregnation with tar or resin, or by other means. Tracks left by worms or dinosaurs, mud-filled burrows, fossil excrement, toothmarks on bones and holes drilled by snails in mollusk shells, deformities produced by parasites, and even objects made or used by animals, including ancient man, must all be regarded as fossils.

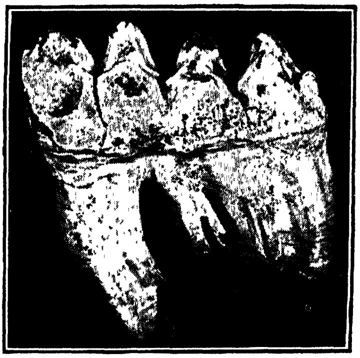

FIG. 117—*Fossil mastodon tooth, showing the enormous cusps on the upper surface. (From a California specimen in the Museum of Geology, University of Michigan.)*

Because fossils are so varied, both with respect to what is preserved and the means of preservation, the following scheme of classification will prove helpful.

1. Fossils giving evidence as to the form or structure of the organism:
   - *A*. With preservation of both form and structure.
     1. Preservation of the actual remains, unaltered.
        - *a* By simple *burial* of hard parts. (Common.)
        - *b*. By *freezing*. (Rare; Siberian mammoths, etc.)
        - *c*. By *desiccation*. (Rare; ground-sloth mummies in caves, etc.)
     2. Preservation of the actual remains, altered by *impregnation*
        - *a*. With *mineral substances*, commonly lime or silica, filling the pores of bones and other hard parts; *permineralized* fossils. (Common; fossil bones that are heavier and denser than fresh bones, etc.)
        - *b*. With *asphalt*. (Rare; animals trapped in tarpits.)
        - *c*. With *resin*, which, on hardening, turns to copal or amber. (Rare; beautifully preserved amber and copal insects, flowers, and other minute fossils, mostly of tertiary age. It should be noted, however, that many amber fossils are really molds, the impregnation not having been complete and the original material having almost disappeared.)
     3. *Petrifaction*, or molecular replacement of the original substance with another material, commonly silica, giving rise to fossils in which fine structural details are preserved, occasionally extending to microscopic cellular structure. (Occasional; petrified wood; limy hard parts changed to flint, iron ore, fool's-gold, phosphate, or other substances.)
   - *B*. With preservation of form alone, details of internal structure lost.
     1. *Molds*. Formed by percolating ground water dissolving away the original object, leaving a hole in the rock that records its form. In the instance of

hollow objects like snail shells, there may be an *external mold* and an *internal mold*, or core; the latter class of objects is often confused with natural casts. (Common.)

2. *Casts.* The interior of a mold may later be refilled with some mineral such as lime or silica, giving rise to a natural cast or *pseudomorph* (false + form), which has the shape but not the internal structure of the original object. A natural cast of a hollow object is formed in the space between the outer mold and the inner mold or core. (Moderately common.)
3. *Imprints.* Thin or soft parts may leave impressions of their form on the upper and lower surfaces of the rock layers that enclosed them, and these imprints may remain after the original object has disappeared or has been reduced to a layer of amorphous carbonized material. (Occasional; the commonest sorts of imprints are those of flat objects such as leaves, insect wings, or fish scales.)
4. *Footprints and trails.* Made on soft mud or wet sand and preserved by being covered with another layer of sediment. (Occasional.)

II. Fossils giving evidence of the existence and activities of organisms but not directly recording their form or structure.

- *A. Coprolites.* Fossil excrement, sometimes giving direct evidence as to the nature of an animal's food and indirect evidence regarding the structure of its alimentary canal. (Occasional.)
- *B. Lesions and deformities.* Such as bone lesions, giving evidence of microorganisms causing disease, and malformations due to the presence of animal parasites. (Relatively rare.)
- *C. Habitations and artifacts.* Worm tubes, the cases of insect larvae, wood showing insect tunnels, mud nests built by insects, mammal burrows, and the like. This category also must include tools and ornaments made and used by prehistoric man. (Relatively rare.)

III. *Fossillike objects* (*pseudofossils*). Objects are occasionally found in the rocks that are mistaken by untrained persons for fossils or are spoken of by geologists as "fossils" through analogy. Among the first class are chemically-formed nodules called *concretions*, which sometimes bear a striking resemblance to organic structures.[1] In the second class are such objects as "fossil" raindrop impressions, "fossil" ripple marks, "fossil" stream courses, and other normally ephemeral features of the physical world that have been preserved in some manner.

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[1] An example is the so-called "dinosaur backbone" shown at the bottom of Silver Springs, Fla., by the guides. This is apparently the edge of a very large flint concretion. There were, of course, no dinosaurs in existence when the Upper Eocene Ocala limestone (in which the spring arises) was formed beneath the sea.

CHAPTER XXVIII

The Older Records of Life

Having seen enough of the geological background to appreciate the time sequences involved, the changing world conditions under which life developed, and the nature of the records from which its history must be deciphered, we are again ready to take up the main thread of the story and to trace the course that life has followed from ancient times down to the present. Here we encounter the usual difficulty of the historian—the necessity of selecting from the mass of available information that which most clearly illustrates the general trends and conditions that he is describing. In so condensed an account of the history of life as ours must be, we shall have to make many broad generalizations to which exceptions could be found, to omit all mention of many interesting and important events, and to depend upon a few selected examples to typify the sort of thing that was going on in all groups of organisms. In thus choosing our materials, we run the risk of making the record of evolution appear more perfect and complete than it actually is, and it should be emphasized that there are great gaps in our knowledge of the history of life. However, little by little and year by year, these gaps are being filled in, and we can feel confident that the picture here presented of the history of organisms is essentially correct in all important points.

We cannot tell the story of life without mentioning kinds of organisms, and their names will mean little unless they call to mind the organism itself and something of its structural pattern and mode of life. Furthermore, it will be necessary to bear in mind the general relationships of the major groups of animals and plants, since, like Genesis, evolutionary history is in large part a record of who begat whom. Frequent reference should therefore be made to the section on the classification of animals and plants (Appendix A).

THE BEGINNINGS OF LIFE

There must have been a time when life on this earth would have been impossible, for geologists and astronomers are now generally agreed that the earth and the other planets were formed as masses of hot gas thrown off from the sun. According to present estimates, this happened some 2 billion 500 million years ago. We do not know how long it took the earth to pass through a molten stage to final solidification or at what time continents and oceans became established on its surface. Life could manifestly not have appeared until after these events and probably not until conditions began at least to approach those of today. How or when life finally did come into existence is still a mystery, but it was certainly at some very early period of earth history. Various hypotheses have been advanced as to the mode of origin of life, but none of them can be tested, and all present difficulties. We cannot, of course, be certain what the first living things were like. It is surmised that they were bits of protoplasm, probably far simpler than most protoplasm now in existence, and perhaps at first almost indistinguishable from nonliving colloidal systems.

The first well-preserved assemblage of organisms is found in the Cambrian rocks, at the beginning of the Paleozoic era. But this is a time far along in earth history, and from the stage of development represented by the Cambrian animals and plants we can be sure that life had then already been in existence for a long time. To find traces of the early history of life, we must turn to the most ancient assemblage of rocks, the "basement complex" of pre-Cambrian times. This basement complex underlies the surface of all the continents, but in most places it is concealed beneath a thick veneer of more recent layered rocks from which most of our knowledge of past life has been obtained. However, in all the continents, there are certain large areas called the *shields*, where the basement complex lies exposed. In North America, the largest such region of ancient rocks is the *Canadian shield*, which surrounds Hudson Bay and extends into New York and the Great Lakes region. Smaller exposures are found where the veneer of stratified rock is locally absent or cut through, as in the Rocky Mountains, the Piedmont and southern Appalachian regions, and in the bottom of the Grand Canyon.

These ancient rocks were formed during the first half or two-thirds of earth history, and in the course of their long existence they have for the most part been profoundly altered by pressure and heat. The rocks that represent the older of the two great divisions of pre-Cambrian time, the Archeozoic era, are prevailingly igneous or are so strongly metamorphosed that we should not expect to find in them any traces of life, even if such traces had once been present. Neither should we expect fossils in the igneous and more strongly metamorphosed portions of the younger Proterozoic formations; but in some regions, beds of almost unaltered Proterozoic sedimentary rocks have been preserved. Here, if anywhere, we may expect to find the evidence of pre-Cambrian life, and many able paleontologists have searched long and carefully for fossils in these rocks. The results have so far been discouraging. The supposed fossils of lime-secreting algae which occur in abundance in some Proterozoic formations and which only a few years ago were cited as the oldest known organisms have lately proved to be of inorganic origin; and in spite of many hopeful announcements the reported discoveries of bacteria, protozoa and arthropods are without good foundation. The only fossils thus far identified with a fair degree of certainty are those of certain blue-green and brown algae, a jellyfish, casts of burrows attributed to annelid worms, and what may be sponge spicules. Because of this scarcity of fossils, the whole of the vast period of time represented by the Archeozoic and Proterozoic rocks has been called the *cryptozoic eon*, or *the age of hidden life*.

As we have already stated, the nature of the Cambrian fauna makes it certain that life must have originated far back in the cryptozoic eon, and the few pre-Cambrian fossils known at least prove the presence of multicellular types. It is possible to infer that by the later part of the Proterozoic, there must have been present unicellular and multicellular algae, naked protozoa, siliceous sponges, primitive coelenterates, annelid worms, primitive brachiopods, and trilobites or their ancestors. Why, then, are there so few pre-Cambrian fossils?

The theories that have been proposed to answer that question are numerous, and we cannot go into them here in any detail. In general the explanations fall into three classes. (1) Fossils were originally present but have been destroyed by the *metamorphism* of the pre-Cambrian rocks. This does not account for the absence of fossils from the relatively unaltered Proterozoic sediments. (2) All the pre-Cambrian strata now accessible were laid down in *fresh water*, at a time when life was still largely marine or at least when any fresh-water organisms lacked skeletons. But the evidence for the fresh-water nature of these sediments is not clear, and they seem too extensive to have been laid down in lakes. (3) For any one of several reasons, the Proterozoic organisms *did not possess skeletal parts suitable for fossilization.* This seems the most likely explanation, and several ingenious hypotheses have been advanced as to why the Proterozoic forms should have lacked skeletons whereas their Paleozoic descendants were so generously provided with them. We shall have to leave the matter at this point; but for a very interesting discussion of the various theories, including one of his own, we refer the reader to *Prehistoric Life*, published in 1939 by Prof. P. E. Raymond, of Harvard University, from which work we have drawn freely in preparing this account. We now turn to a consideration of the first well-known organisms, those of the Cambrian, after which we shall be in a better position to estimate the amount of evolution that took place during the cryptozoic eon.

THE LIFE OF THE CAMBRIAN PERIOD

The cryptozoic eon closed with a great "revolution," accompanied by world-wide uplift of the continents and withdrawal of the seas. There followed a very long interval for which the record is lacking, since the continents were being profoundly eroded and the sediments thus produced were deposited in the inaccessible depths of the sea. When the seas finally came back over the lands in Cambrian time, their sediments, resting on the eroded surfaces of the cryptozoic rocks, were filled with a profusion of fossils. This return of the seas marked the start of a new era—the *Paleozoic*, or *age of ancient life*—and the real beginning of the well-documented history of life.

The record of the Cambrian and the two succeeding periods of the Paleozoic is essentially that of marine life. So far as can be determined, the lands were lifeless, although tidal flats and moist ground may have supported growths of algae. In marked contrast to the barren lands, the seas literally swarmed with life. Among plants, there were many kinds of floating unicellular and multicellular algae, attached seaweeds, and lime-secreting algae which formed reefs. Snails were present in the early Cambrian, and bivalve mollusks and primitive cephalopods made their appearance before its close. There were many kinds of sponges, a few jellyfishes and echinoderms, and an abundance of marine worms and simple crustaceans. The dominant animals of the time were the trilobites (an extinct group of Crustacea) and the brachiopods, or lamp shells, both of which existed in great numbers and variety. All told, over 1,200 different species of Cambrian animals have been described from North America alone.

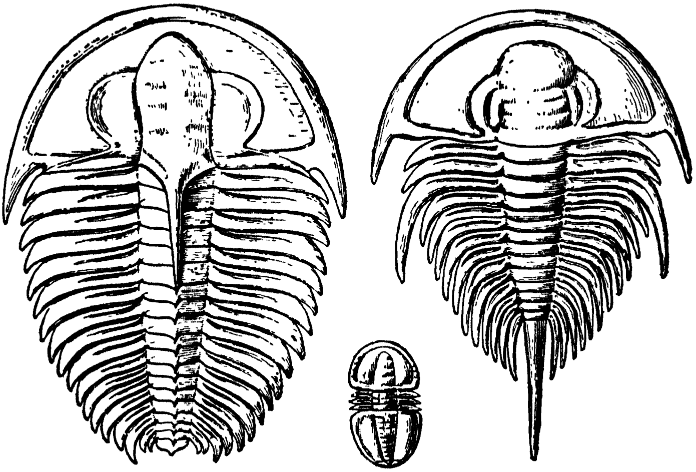

FIG. 118.—*Characteristic lower Cambrian trilobites.* (*From Pirsson and Schuchert, Textbook of Geology, John Wiley & Sons, Inc.*)

We should know far less about the life of this period were it not for a fortunate accident by which many of the more delicate creatures were preserved. In the shallow, quiet seas of what is now British Columbia, there were evidently depressions in the sea floor, in which the water stood stagnant, losing its oxygen and becoming loaded with carbon dioxide and ammonia produced by the decay of organic material on the bottom. These depressions were death traps for organisms that entered them. The remains of these, protected from scavengers by the oxygenless water, were buried in soft black mud, which preserved imprints that show the forms of the organisms and sometimes even the finer details of their structure. This mud is now the Burgess shale, of mid-Cambrian age, exposed high on the flank of Mount Wapta at an elevation of 8,000 feet above the sea.

From this deposit, there have been described over 130 species of organisms, most of which have not been preserved elsewhere. They are mostly swimming and floating types with relatively soft bodies, and they merely hint at the large numbers of Cambrian animals and plants that remain unknown to us. Among the Burgess shale fossils are seaweeds, sponges, at least one jellyfish, and a remarkable array of annelid worms in which the entire body form, bristles and scales, and often the digestive tract are preserved. The most interesting organisms, however, are the crustaceans—shrimplike forms, trilobites, and others intermediate between Crustacea and Arachnida. One of the fossils is a wormlike creature, related to the "living fossil" Peripatus, which appears to link the annelid worms with the arthropods. A striking feature of the fauna is that the usual bottom-dwelling creatures seen in other Cambrian deposits, such as the brachiopods, snails and hard-shelled trilobites, are rare; they could not live in such an environment and were less likely to enter by accident than were the floating and swimming species.

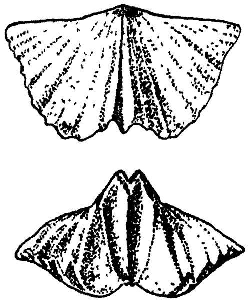

FIG. 119. *An Ordovician brachiopod, Platystrophia.*

Here in the Cambrian, we see the *oldest well-known assemblage of organisms.* They are a diversified lot; most of the animal phyla that would be expected to leave fossils are represented, with the outstanding exception of the chordates, and, although among plants only thallophytes are present, they are of various types. The fossil record of later times shows clearly that the Cambrian animals and plants gave rise to all later types. They were not simple, but neither were they so complex and highly organized as those of today, and many groups were missing. From the Cambrian to the present, a great amount of evolution has evidently taken place, and it is therefore reasonable to suppose that these Cambrian types of life in turn arose from still simpler ones and in the end probably from a single primordial protoplasm. We have not, then, merely pushed special creation back some hundreds of millions of years to the Cambrian but must suppose that life and evolution had already had a long cryptozoic history leading up to the Cambrian fauna. Let us see what can be deduced as to this pre-Cambrian evolution from a consideration of the Cambrian organisms and the few late cryptozoic fossils. The major accomplishments of life prior to the Cambrian may be listed as follows:

1. *Cell organization had been perfected.* This was the greatest step in the history of life, since all later evolution has been based upon the cell as the unit of structure and function.

2. *Plants and animals had been differentiated,* with the development of chlorophyll and its use for the manufacture of food by some organisms and the acquisition of the habit of food capture by others.

3. *Cell aggregations had developed,* with corresponding specialization and division of labor among the cells. This involved segregation of germ and soma and the introduction of death of the multicellular individual as a normal part of the life process. It made possible the next step.

4. *The principal animal phyla had already arisen* and become stabilized, with the exception of the Chordata. Although only the lowest members of these groups were present in the Cambrian, the main structural types of the animal kingdom, except as noted, had already been established.

5. *The lime-secreting habit had been developed* among many groups of animals and some of the plants. This involved the use of a cell product (lime phosphate or carbonate, perhaps originally an excess material that had to be excreted) to form structural elements used for support, locomotion, or protection. The habit first appeared among and is especially marked in sedentary forms, suggesting that the active types were better able to excrete their excess lime. Ability to use lime for skeletal purposes seems to have developed during the long interval between the late Proterozoic and the Cambrian and affords a partial explanation for the sudden increase in abundance of fossils in the Cambrian rocks.

Certain biologists, impressed with the high degree of internal organization shown by the cell, have maintained that the time necessary for the perfection of the cell from the incomparably more simple first living material may have been as great as that required by all subsequent evolution. This is an extreme view and would require life to have originated far back in the Archeozoic, perhaps 500 million to 1,000 million years before the beginning of the Cambrian. There is nothing to show that life may not have come into existence as late as the beginning of the Proterozoic. However this may be, as soon as the development of organized cells made possible cell aggregations and hence multicellular animals and plants, the pace of evolution undoubtedly speeded up, and it need not have been long in a geological sense before the principal structural types had been established among animals. As life has become more abundant and as the variety of organisms and the complexity of their interrelationships have increased, the rate of evolution seems to have continued its acceleration—perhaps as a result of increasing competition and more and more rigorous selection.

It is an interesting fact that with the exception of the Chordata, which appeared early in the Paleozoic, no new animal phyla have arisen since the Cambrian. It seems unlikely that all the possible patterns of organization went into the formation of the small number of phyla that actually developed. It may be that with the available life niches already well-occupied by animal types far along in organization and adaptation to their environments, there was simply no chance for newcomers to get a start. Post-Cambrian evolution has been largely an elaboration, branching out, and replacement of older by more modern types, *within* the main lines already laid down during or prior to the early Paleozoic.

LIFE DURING THE ORDOVICIAN AND SILURIAN PERIODS

The record of life during the two periods following the Cambrian is still almost wholly that of the seas, in which the invertebrates continued to be the dominant forms. Ordovician life, compared with that of the Cambrian, was more diversified and abundant, and additional types appeared in the Silurian. Trilobites and brachiopods continued to be present in large numbers, though the trilobites began to decline in the Silurian. Among the new groups which appeared in the Ordovician or which were represented only in the last of the Cambrian are the colonial graptolites and corals among the coelenterates; the bivalves, cephalopods, and chitons among the mollusks; the bryozoans; the crinoids and other stalked forms, starfishes, and sea urchins among the echinoderms; and eurypterids and barnacles among the arthropods. The phylum Chordata also made its first appearance in the Ordovician, as will be described later.

The *graptolites* were among the most characteristic of the Ordovician animals. The history of their rise and fall is of interest, both because it is typical of what happened to many another group and because this is one of the few entirely extinct assemblages in which the reasons for early success and later extinction seem clear. The fossils of these animals are especially abundant in the black Ordovician shales and look like small, shiny pencil lines drawn on the surface of the rock; the name *graptolite* means "written stone." On close examination, one or both edges of the line are seen to be saw-toothed. Graptolites were hydrozoan coelenterates that formed branching colonies of small polyps. The stalk and branches were threadlike, with the polyps ranged along the branches in straight rows; the serrated edges of the fossils mark the positions of the individual polyps.

The earliest graptolites to appear were many-branched bushy colonies that grew upright on the sea bottom. Later, some of them began to hang downward from floating seaweeds, and eventually types appeared that produced their own bladderlike floats. At the surface of the sea, these drifting types found freedom from enemies and an ample supply of minute food organisms. They flourished exceedingly, becoming abundant and rapidly spreading to all parts of the oceans. Their branches were supported by fragile threads, easily broken by waves, and these detached branches rained down everywhere on the sea floor, to be eaten by trilobites or other animals or to be buried in the lifeless black oozes that later became the black shales.

Unfortunately for the graptolites, by the close of the Silurian, many free-swimming predacious animals had developed, which probably found these floating organisms an abundant source of food. They seem to have eaten the graptolites faster than the latter could reproduce, for the floating types rapidly disappeared. The more conservative bottom-dwelling species never became abundant, probably because of the numerous animals that fed upon them; but they did survive until the Devonian, outlasting their more specialized and temporarily more successful relatives.

The *aquatic arachnids* of the early Paleozoic included some of the most active and successful animals of their day. They evidently arose from trilobites, since their bodies show many trilobitelike features, and they included the ancestors of our modern spiders, scorpions, and their allies. They early split into two lines—the king crabs and the eurypterids. The king crabs, represented today by the common horseshoe crab of our beaches (Limulus), first appeared in the late Cambrian and by Silurian times had developed into forms not unlike our modern one.

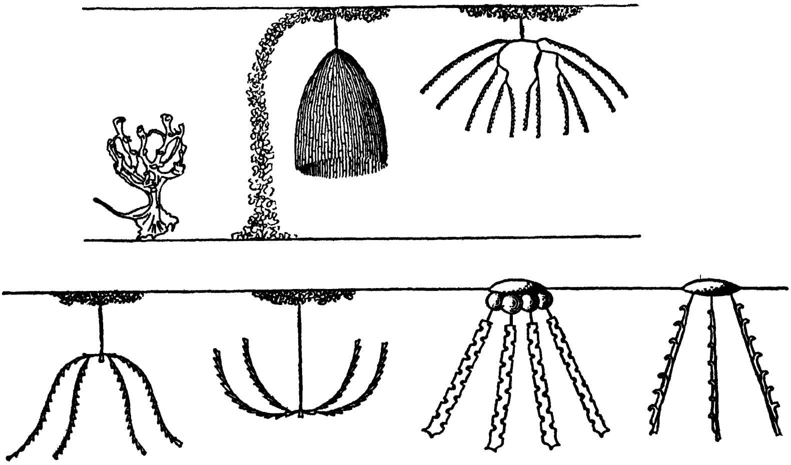

Fig. 120.—*Stages in the evolution of the graptolites.* (*From Raymond, Prehistoric Life, reprinted by permission of the President and Fellows of Harvard College.*)

The *eurypterids* were much the more numerous and important. They had elongated bodies, composed of a small cephalothorax and a segmented abdomen, which was broad anteriorly and narrow posteriorly like that of a scorpion. As in all arachnids, the first pair of appendages was pincerlike, whereas in the Crustacea, which they somewhat resembled, the first appendage is always feelerlike. Most of these animals were fairly small, averaging about a foot in length, but some of the later types were large; Pterygotus, of the Devonian, reached a length of 9 feet, and was probably the largest arthropod that ever existed. Eurypterids could crawl about, and most of them had swimming paddles. The group appeared in the Ordovician and was most abundant in the Silurian and Devonian, though a few forms survived until the Permian. The earliest eurypterids are believed to have been marine, but the latest were certainly inhabitants of fresh water. The decline of the group coincided with the rise of the amphibians and reptiles, which may have fed upon eurypterids.

Although the eurypterids have long been extinct, our modern scorpions are their direct descendants, relatively little changed except for having a sting in the tail and being equipped to breathe air. It is, therefore, of considerable interest that fossil scorpions have been found associated with eurypterids in the Silurian rocks. These were long regarded as the most ancient air-breathing animals known, but the absence of book lungs such as are present in modern scorpions proves that they were aquatic; terrestrial scorpions are first known from the Carboniferous.

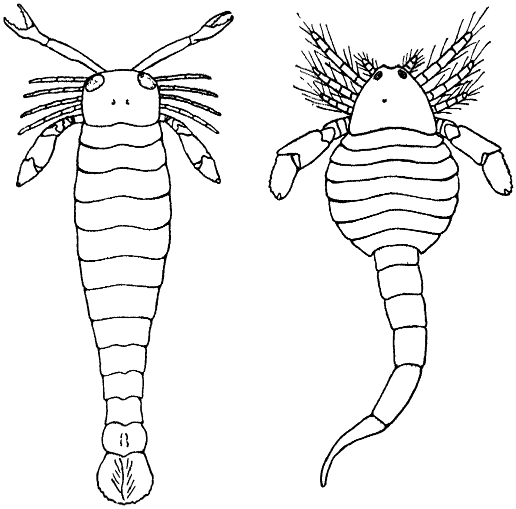

FIG. 121. *Silurian eurypterids. On the left Pterygotus, a very large form with long pincers and swimming tail; on the right Eusarcus, a swimming and crawling form with scorpion-like tail. (From Pirsson and Schuchert, Textbook of Geology, John Wiley & Sons, Inc.)*

One of the most important events in the life of the early Paleozoic was the appearance of the phylum Chordata. The first traces of this group are some fragmentary fossils of simple fishlike organisms found in upper Ordovician rocks. The oldest well-preserved chordate fossils are from the late Silurian, and these include a number of types of primitive fishes that are grouped under the name *ostracoderms*. All these evidently possessed a notochord, but they lacked jaws and an internal skeleton. Most of them had the anterior part of the body enclosed in a boxlike armor of massive skin plates, the rest of the body being fishlike, covered with scales. The ancestry of these earliest chordates is still shrouded in mystery. Various attempts have been made to show how they could have been derived from annelid worms or from some group of the arthropods—eurypterids or trilobites. In the light of embryological evidence, it seems most likely that they are related to the echinoderms, and it is therefore of interest that in the simplest group of ostracoderms, a number of features of resemblance to primitive, bilaterally symmetrical ancestral echinoderms have recently been traced.

Evidence of the existence of terrestrial organisms is lacking in the Ordovician rocks; but the oldest known land plants have been found in the Silurian—a few imperfectly preserved remains of simple mosslike forms. Air-breathing animals have not been found in either period, the supposedly terrestrial Silurian scorpions and millipedes being now regarded as aquatic.

LIFE DURING THE DEVONIAN PERIOD

In the Devonian seas, trilobites were few and snails and bivalve mollusks but poorly represented. The cephalopod mollusks were on the increase, and corals, brachiopods, and echinoderms were abundant and varied. But the dominance of the invertebrates was over; the Devonian was the *age of fishes.* It was also the period that saw the *first abundance of land life* and the emergence of *four-footed, air-breathing vertebrates.*

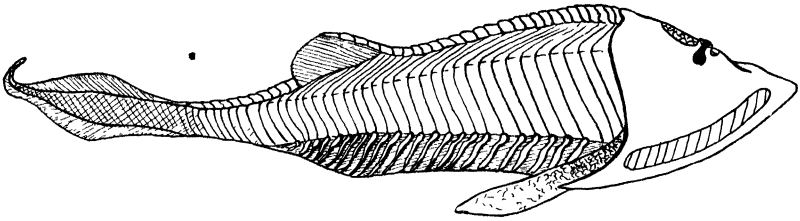

FIG. 122. *A Devonian ostracoderm, Cephalaspis.* (*Redrawn from Newman, The Phylum Chordata, The Macmillan Company*)

The Devonian Fishes. Judging from the great numbers of fossil fishes that occur in some of the Devonian strata, the seas and fresh waters of this age must have swarmed with fish life. The chief groups represented were the *ostracoderms,* which reached their climax in this period, and a number of newly arrived types—the "spiny-finned sharks," true sharks, the aberrant arthrodires, and a variety of primitive "bony fishes." The ancestors of all these are to be sought among the ostracoderms of the Silurian and early Devonian. Some of the ostracoderms possessed dermal plates and scales similar to the placoid "scales" or denticles of sharks; others had an armor suggesting that of the otherwise isolated arthrodires; and still others have been regarded by some students as ancestral to the bony fishes. It is more likely, however, that the latter arose indirectly through sharklike descendants of ostracoderms.

There is good reason to believe that the "sharks" and the ancestral bony fishes were evolved in the fresh waters, presumably in the large rivers. The sharklike types went out into the sea quite early and their descendants have ever since been mostly marine. Having always inhabited open water, none of the sharks and their allies ever developed lunglike structures. The majority of the bony fishes, on the other hand, seem to have moved up the rivers and into the swamps and ponds that fed them. This has been inferred partly from the nature of the rocks in which their remains are found and partly from the changes that occurred in their respiratory mechanism. *All the bony fishes developed lungs* for breathing air, in addition to their gills; the environmental conditions that favored this evolutionary modification are discussed later.

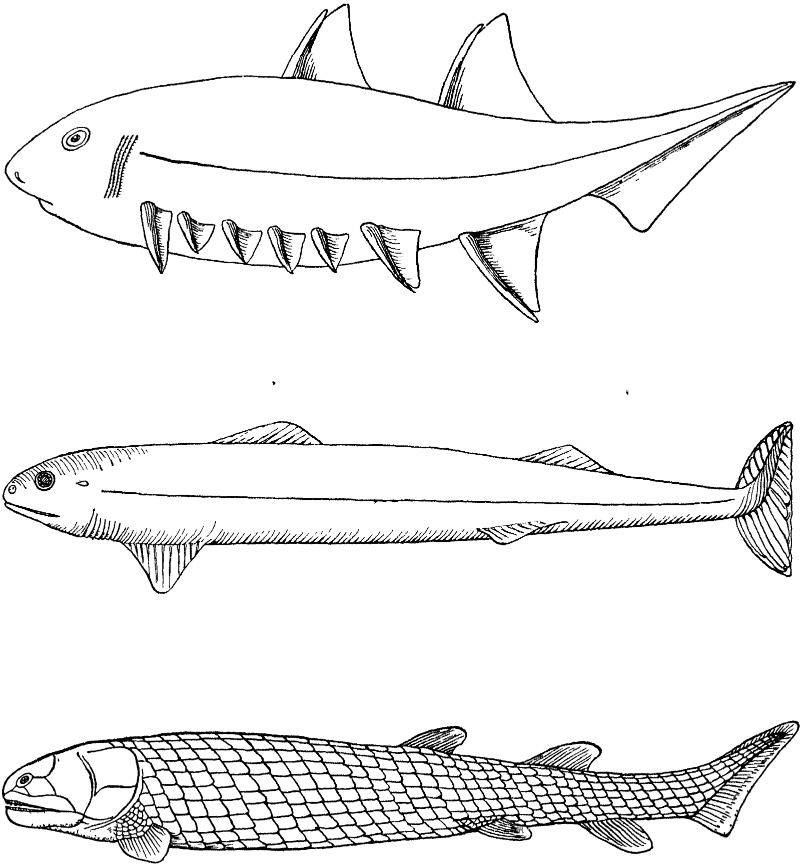

FIG. 123. *Devonian fishes. Upper figure, a spiny-finned shark, Climatius; middle figure, a fast-swimming marine shark, Cladoselache; lower figure, a middle Devonian lobe-finned "ganoid" fish, Osteolepis. (Redrawn from Pirsson and Schuchert, Textbook of Geology, John Wiley & Sons, Inc.)*

Aside from the ancestral bony fishes, the principal Devonian types were the "spiny-finned sharks," primitive true sharks, and arthrodires.

All these had a cartilaginous skeleton and a primitive type of tail, in which the tapering end of the body extended into the dorsal tail lobe. The oldest and most primitive of them were the *spiny-finned sharks,* which lived in the rivers along with the later ostracoderms and were mostly small. These had a variable number of small paired fins, supported at the anterior edge by stiff spines. The spines are common fossils in the fresh-water Devonian rocks. Later in the period, the earliest *true sharks* appeared, probably descended from some of the "spiny-finned sharks"; these migrated into the sea and there became numerous. Like modern sharks, they had an incomplete surface armor of small denticles imbedded in a tough skin. These denticles, sometimes called *placoid scales,* have a structure quite like that of a tooth, with a pulp cavity enclosed in dentine and a surface layer of hard enamel. From such denticles, arranged in rows along the margins of the jaws, we can trace the development of the vertebrate tooth. These ancient sharks had the first true teeth, and there can be no doubt that the teeth of the higher vertebrates have been derived from the denticles of their sharklike ancestors.

The *arthrodires* were the strangest fishes of the Devonian and included the largest and most powerful animals of the time. The anterior part of the body was covered with a heavy armor—that of the head in one piece and that of the trunk in another, with a hinge joint on each side of the neck. Dinichthys, the "terrible fish," had a body 12 feet long and a skull nearly 3 feet across; Titanichthys probably reached a length of 20 feet. These fishes were unlike any other vertebrates in that they bit, not with the lower jaw but by raising the whole top of the head on the neck hinge and bringing it down on the rigid lower jaw. The jaws were armed with fearful "teeth," which were really not teeth at all but projecting bones of the head. The arthrodires are the only known vertebrates that actually used their jawbones for biting instead of having teeth or horny blades. Although they were the rulers of the late Devonian and early Mississippian seas, for some unknown reason the group suddenly disappeared.

The *bony fishes* of the Devonian soon became abundant and varied. When we get our first glimpse of them in the mid-Devonian, they had already differentiated into three main stocks—the "lungfishes"[1] (Dipnoi), the lobe-finned fishes (crossopterygians), and the ray-finned fishes (actinopterygians). All these early fishes were "ganoids," *i.e.,* their bodies were covered with a heavy armor of close-fitting scales, made of bone, with an outer layer of enamel (ganoin). The scales were usually diamond-shaped, though sometimes circular, and overlapped like tiles, often with interlocking processes. Such an armor may be seen today in the gar pikes, which are surviving "ganoids."

The three groups of Devonian bony fishes have had quite different fates. The *lungfishes* were numerous until the end of the Paleozoic but gradually declined until today they are represented by only three surviving genera. They are not now regarded as the ancestors of the amphibians, though this view was held for a long time; their peculiar fan-shaped teeth and their elongate fins with a central axis could scarcely have been converted into the amphibian tooth and leg. Such resemblances as they show to amphibians are probably the result of their common origin with the *lobe-finned fishes*, of which we shall have more to say later.

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[1] The name *lungfishes* is an unfortunate choice for the Dipnoi, since the other primitive bony fishes also possessed lungs.

The *ray-finned fishes* have been the most successful group as fishes and for a long time have dominated the sea as well as the fresh waters. The ancient "ganoid" ray fins gave rise to the modern *teleosts* during the Jurassic, and the latter now include by far the greater number of existing fishes. In the teleosts, the primitive lung has been converted into a hydrostatic air bladder; the scales have become thin and horny and lack enamel; the tail has lost all trace of its original up-bent tip; and many changes have occurred in the skeleton and other body parts.

The Origin of the Amphibians. We have already mentioned that the ancestral bony fishes had developed a lung by means of which they could breathe air. There are two theories as to why this should have occurred. We know that the Devonian was a time of disturbed conditions, during which several great mountain ranges were formed and great land deltas were built at the foot of the rising mountains both in North America and in Europe. Great thicknesses of red sandstones were deposited, and the remains of whole schools of fish are sometimes found in these rocks. According to one view (the older), red rocks are a sign of *aridity*, and the Devonian climates were supposed to have been at least seasonally dry. At times of drought, the pools and lagoons would become overcrowded and foul, with the water low in oxygen and the food insufficient. This would account for the great mortality observed among the fishes and at the same time would have put a premium upon the ability to breathe air; fishes that had this capacity would be at a great advantage in the struggle to survive from season to season. If, in addition, they had had fins that would carry their weight as legs, they would have had the additional advantage of being able to quit the water in search of food or more favorable environments.

This is, of course, only a theory, but it seems to fit most of the facts. However, it now seems very doubtful whether the red beds of the Devonian really indicate the occurrence of arid conditions at the time of their formation; more likely they were rapidly accumulated during a time of warm and moist climate, in the form of alluvial fans, or land deltas. On such fans, the streams are continually changing their courses; pools and swamps are formed in which periodic overflow is followed by drying up; and under such conditions, the same effects might be produced as under the theory of arid Devonian climates. One or the other of these explanations is probably the right one, and in the light of the habits of certain living fishes that we shall now consider, they do not seem farfetched.

At the present time, there are five genera of primitive fishes that breathe the air and live under conditions similar to those postulated for the Devonian. Three of these genera are lungfishes—Neoceratodus, with one Australian species; Protopterus, with three African species; and Lepidosiren, with one South American species. The two other genera of lung breathers are Polypterus and Calamoichthys, found in the Nile, Congo, and other African rivers emptying into the Atlantic Ocean. These are not "lungfishes" but surviving representatives of the primitive "ganoid" ancestors of the ray fins. For a long time, they were thought to be the last of the lobe-finned fishes, the group from which the Amphibia developed, but the structure of their fins and lack of internal nostrils (present in lungfishes and lobe fins), with other characters, makes this

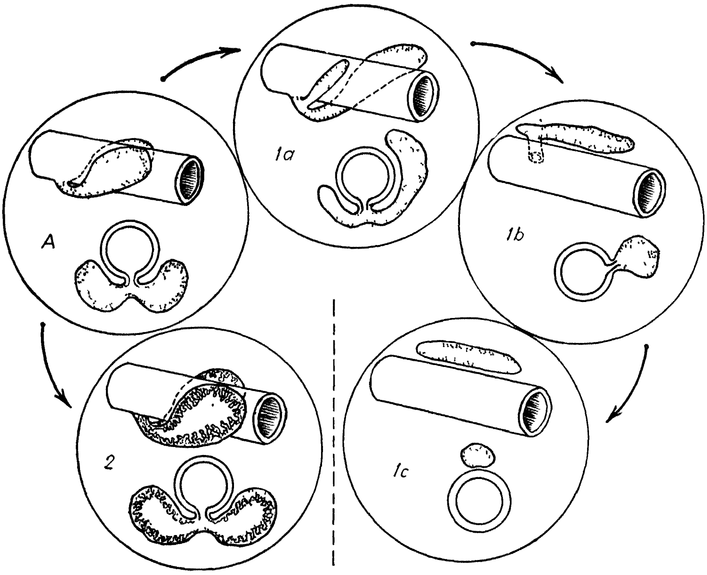

FIG. 124. *Diagram showing the mode of origin of the lungs of terrestrial vertebrates* (*2*) *and the swim bladder of the teleost fishes* (*1c*) *from the primitive condition in the Devonian "ganoids"* (*A*). *The unshaded tube represents the oesophagus; the shaded lobes the air sacs, as seen from the left side and in cross section.* (*A*) *The primitive condition in the Devonian "ganoids"*; (*1a*) *The modern lung-fish Polypteris, right lung larger than left;* (*1b*) *Erythrinus, left lobe rudimentary and turned forward, opening to eosophagus shifting toward dorsal position;* (*1c*) *advanced condition in teleost fishes, connection of swim bladder with oesophagus lost;* (*2*) *the lungs of terrestrial vertebrates, derived from A, with increased interior surface area.* (*Modified from Kingsley, Comparative Anatomy of Vertebrates, The Blakiston Company.*)

view untenable. Each of these five genera possesses an air bladder that opens into the esophagus and is richly supplied with blood vessels; it is better developed in the lungfishes than in the two primitive ray fins, and is paired in Protopterus. This organ is a true lung, which functions either in connection with the gills or alone.

The Australian lungfish Neoceratodus lives in pools and water holes, cropping the aquatic vegetation for the sake of the snails, insects, and other small animals found thereon. During the dry seasons, the pools often become stagnant, low in oxygen, and foul with the decaying bodies of other fishes; but this does not seem to bother the lungfish in the least, though at such times they depend wholly on their lungs for air. The African Proptopterus and the South American Lepidosiren live in marshes bordering rivers, where they feed on frogs, insects, and other animals. During the wet season, they live much as does Neoceratodus, although they are still more dependent upon their lungs and will drown if prevented from coming to the surface. During the dry season, when the marshes may be dry for months at a time, these fishes burrow into the mud and coil up at the bottom of the hole. There they secrete around themselves a moisture-holding "cocoon" of slime, tightly closed everywhere except over the mouth; and there they stay, breathing air and kept moist by their slimy covering, until the return of water to the marshes. The existence of habits such as these among primitive fishes of today makes our guesses about the habits of their Devonian ancestors seem not only reasonable but more than probably correct.

As we have said, neither the lungfishes nor the ray fins can be regarded as the ancestors of the amphibians. This honor must go to the lobe-finned "ganoids," which, though relatively unsuccessful as fishes, gave rise to the first land vertebrates. The lobe fins were the most abundant of the "gancids" during the Devonian, and thereafter declined until their extinction in the Mesozoic. They are the fishes that seem to have pushed farthest into the precarious habitats of the marshes, ponds, and shifting streams. Other fishes as well as lobe fins had lungs, but *the*

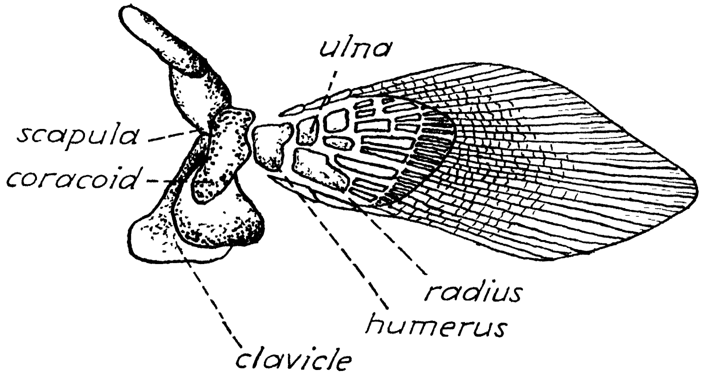

FIG. 125. *Right anterior fin of the lobe-finned Devonian fish, Sauripterus, showing the elements of the pentadactyl limb of the terrestrial vertebrates present in the basal portion. (From Lull, Organic Evolution, The Macmillan Company.)*

lobe fins alone had the type of fin that could have been transformed into the amphibian leg. This it was, in all probability, which enabled them to evolve into land animals. The fins of certain of the fossil genera have a fleshy base, within which are imbedded cartilaginous supports, the arrangement of which corresponds closely with that of the bones of the vertebrate limb. Beyond the base the fins spread out into a swimming blade. It is thought that as these fish became more and more adapted to crawling, the distal (swimming) part of the fins was bent up out of the way, with the weight of the fish supported on the lower side of the joint between the base and the swimming blade; as the latter was less and less used, there would be nothing to prevent it from eventually disappearing entirely, while the useful part of the fin was strengthened and improved to form a walking leg.

Whatever we may think of these theories as to how it happened, there can be no doubt that some ancient lobe-finned fish was the actual ancestor of the earliest amphibians. Indeed, except for the possession of legs, the oldest of the amphibians are scarcely distinguishable from lobefins. Though land dwellers themselves, the amphibians have to return to the water for reproduction and go through fishlike aquatic stages very like the young of modern lungfishes. We do not know what the young of lobe-finned fishes were like, but they were probably very much the same as those of lungfishes. The first true *amphibians* (Stegocephalians) appeared in the late Devonian, for remains of these animals have recently been found in rocks of this age in Greenland. Previously we had to base our statement that they arose in this period on a single footprint from the Devonian of Pennsylvania. These are the *first fossils recording the existence of land vertebrates.*

The First Forests. The development of a land fauna was, of course, dependent on the prior establishment of a land flora, which would serve as the basic food supply for animals. It is significant that the period in which the first land vertebrates arose was also the time when the first air-breathing scorpions, insects, "thousand-legged worms" (diplopods), and snails are known or thought to have appeared on the scene, and that this coincided with the development of the first abundant land vegetation. In the early Devonian, the only land plants were still small, simple forms without leaves or true roots—thallophytes, bryophytes, and the earliest and most primitive of the pteridophytes. Sometime during the middle Devonian, true ferns and other higher pteridophytes arose, and by late Devonian, true forests had come into existence for the first time. One of the most remarkable examples of these forests was found at Gilboa, N. Y., where more than 30 great stumps and the spreading roots of tall trees were discovered still standing in their native soil, now transformed into rock. These trees attained a height of about 40 feet, and are thought to have been seedferns. Other members of the Devonian forests were the giant horsetails, scale trees, and primitive conifers. Thus the Devonian, in which vascular plants arose and became dominant on the lands, is fully as important a period in the evolutionary history of plants as it is in that of animals.

LIFE DURING LATE PALEOZOIC TIME

Although geologists usually divide the late Paleozoic into three periods, the Mississippian, Pennsylvanian, and Permian, we shall recognize only two—the Carboniferous and the Permian. The *Carboniferous period* was the coal age, whence its name. The outstanding events of this period were the development of the luxuriant coal forests, the appearance of winged insects, the climax of the amphibians, and the coming of the first reptiles. During the *Permian period*, there occurred one of the great revolutions, marking the end of the Paleozoic era and bringing changes in environment that resulted in extinction for many groups and new opportunities for others.

The Carboniferous seas contained abundant and varied life, the sea lilies and other echinoderms, corals, and cephalopod mollusks being especially numerous. Sharks and "ganoid" fishes were present in large numbers. But the brachiopods, though still common, were almost at the end of their dominance; the trilobites were nearly gone; and many another ancient group was dwindling or had already disappeared. From this time on, we shall be unable to pay much attention to marine life, on account of the increasing importance of what was occurring on land. This is not because the scene of the evolutionary spectacle shifted altogether to the lands but simply that we cannot watch both rings of the circus at once.

The Coal Forests. During the upper Carboniferous (Pennsylvanian), much of the surface of the lands lay near sea level, rising and lowering a little at intervals, so that sometimes a low, wet land was exposed and at other times shallow seas came flooding in. Vast swamps covering thousands of square miles developed, covered with a dense forest growth. In general aspect, these swamps probably resembled the Okefenokee and Great Dismal swamps of today, but they were of much greater extent, and their vegetation was of unfamiliar types. The dominant plants were the scale trees (Lepidodendron and Sigillaria), the giant horsetails (Calamites), various trees with fernlike leaves (some probably true tree ferns but the majority seed ferns), and the large-leaved evergreen trees (Cordaitales).

Remains of these and other plants, accumulating as water-logged masses in the same way in which peat is now formed, were buried from time to time under layers of mud brought in by temporary invasions

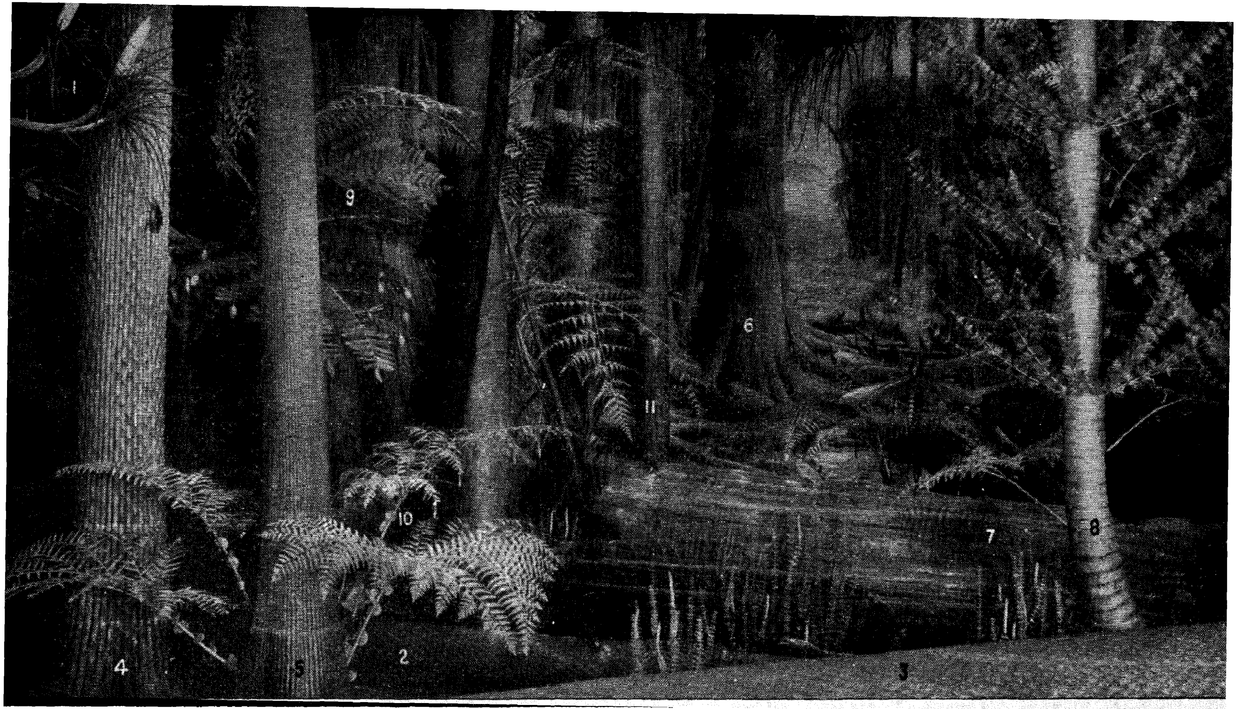

FIG. 126. *Restoration of a Carboniferous swamp forest, based almost entirely upon actual fossil specimens obtained in the Illinois coal fields.* (1) (2) (3) *Lepidodendron;* (4) (5) (6) (7) *Sigillaria;* (8) *Calamites;* (9) (10) *seed ferns;* (11) *Cordaites. Several true ferns and various smaller plants are also shown.* (*Courtesy of the Field Museum of Natural History.*)

of the sea. Today these swamp deposits are the coal beds. Where they were merely compressed by the weight of later deposits, they have become soft coal, and the beds contain fossils; but where they were caught during the Permian in the squeeze that folded up the Appalachian Mountains, they became metamorphosed into anthracite, in which nearly all traces of fossils have been destroyed.

The First Winged Insects. In these ancient coal forests, there lived an abundant fauna, dominated by the oldest known insects and by the stegocephalians. The insects belonged mostly to two groups—the primitive winged insects (Paleodictyoptera) and the ancestors of the cockroaches. Both these groups had well-developed wings and were evidently far long in insect evolution. The simplest insects surviving today are wingless and show no signs of ever having had wings, and it is certain that the original insects were likewise wingless. This means that insects must have had a long evolution prior to the period of abundant winged forms in the coal forests; they may well have developed during the Silurian or Devonian.

Many of the Carboniferous insects were very large, the greatest having had a wing spread of about 2 feet. It used to be supposed that all the ancient insects were large compared with those of today, but more recent discoveries have demonstrated the presence of many small forms as well. None of the modern groups was yet in existence, and none of the Carboniferous insects had a pupal stage in the life history.

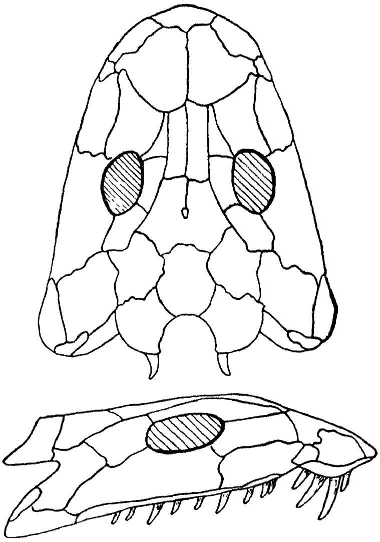

FIG. 127. *Dorsal and lateral views of the skull of a stegocephalian amphibian, showing the completely roofed-over skull and the series of bones in the temporal region back of the eye. (From Schuchert and Dunbar, Textbook of Geology; John Wiley & Sons, Inc.)*

The Dominance of the Amphibians. The amphibians had become quite abundant since their first appearance in the Devonian, nearly 100 species of various sizes and forms being known from the Carboniferous. All had a boxlike skull, completely roofed over except for the eye orbits and nostrils. This accounts for their name *stegocephalians,* which means "roof-headed." The vertebrae were partly cartilaginous and composed of several parts—a condition unknown among modern amphibians and higher vertebrates, and showing the close relationship of the stegocephalians to the fishes. The legs were short and weak, sprawling out at the sides of the body.

Most stegocephalians were apparently amphibious inhabitants of fresh-water swamps; they were generally rather stout-bodied, with short tails and bellies protected by bony plates, upon which they rested except when walking. A few had gone back to the water entirely and were similar in form to our salamanders, and one group became marine. The immature stages of all were aquatic and fishlike, as is true of the modern amphibians. The limitations of the stegocephalians were that they were tied to the water by their reproductive requirements, that their skin offered no adequate protection from drying, and that their sprawling legs made progress on land slow and clumsy.

The First Reptiles. The most primitive known reptiles lived, like the stegocephalians from which they developed, in the late Carboniferous swamps. Although they resembled Stegocephalia, we can recognize them as reptiles by certain changes that had taken place in the skeleton, especially the skull. In these early reptiles, the three basic inventions that account for the later dominance of the group had their beginnings. The first was a change in the *position of the legs*, drawing them closer in to the sides of the body and preparing the way for the supporting, pillar-like leg which made possible efficient locomotion on land and which is found in all the higher terrestrial vertebrates. The second was the development of *scales*, which served to prevent undue evaporation in dry air and which survive as scales, feathers, or hair in all the higher groups. The third, and by all odds the most important, was the invention of the *shelled egg*, by means of which the reptiles were emancipated from going back to the water for reproduction. This change, of course, does not show in the fossils but may be inferred from the indications of comparative anatomy and embryology and from the fact that fossil eggs laid by some of the Mesozoic reptiles have been discovered.

The *shelled egg* is really a combination of several inventions; the *yolk sac*, or embryonic stomach, found in fishes and Amphibia as well as in the reptiles; the *allantois*, a new organ enabling the imprisoned embryo to breathe and to dispose of wastes; the *amnion* and *chorion*, enclosing the embryo in what is the equivalent of a private lake that takes the place of the original aquatic environment; and finally, *internal fertilization*, eliminating the necessity of an aquatic environment for the functioning of the spermatozoa, and permitting the spermatozoa to reach the egg before the eggshell is formed about it. Animals with such a reproductive mechanism could for the first time leave the vicinity of ponds and streams and take full possession of the land.

During the late Carboniferous, the reptiles became fairly numerous, forming a group called the *cotylosaurs*. Within this group there were varied lines of modification, and from some of the diverse cotylosaurs are believed to have developed the different reptile stocks discussed in connection with Mesozoic history.

CHANGES IN LIFE DURING THE PERMIAN

The spilling off of the Paleozoic seas in late Carboniferous was merely the first symptom of the coming of one of the great "revolutions" that mark the close of eras. This, the *Appalachian revolution,* reached its climax in the Permian period, during which all the continents were strongly elevated, the Paleozoic sediments in the Appalachian trough were folded into a range of mountains comparable in grandeur to the modern Himalayas, a second generation of Paleozoic Alps was uplifted in Europe, and a profound and world-wide change in climates set in. The mild, moist conditions that had prevailed through most of the Paleozoic were replaced by cooler and drier climates. Starting apparently with the Antarctic region and spreading eventually into Australia, South America, Africa, and even as far as India, tremendous glaciers covered large parts of the Southern Hemisphere. Widespread glaciation did not occur in the Northern Hemisphere, but the climate there became dry and cold. The change in life conditions was so extreme that a great many of the old groups of plants and animals did not succeed in adjusting themselves to it and became extinct.

The effects of this revolution were felt in the seas as well as on the lands, for the oceans were cooled and the shallow parts of the ocean were restricted to the edges of the continents instead of being spread out over large areas. In the crowded marginal seas, competition and unfavorable environment killed off a host of Paleozoic stocks. The last trilobites were wiped out; the brachiopods suffered a blow from which they never recovered, as did the sea lilies and the old types of corals; even the cephalopod mollusks were reduced to a few types, which, however, survived to give rise to the dominant ammonites of the Mesozoic.

On the lands, the effects of the change were more severely felt, with an even heavier mortality of the Paleozoic types of life. The majority of the plants characteristic of the coal forests disappeared, although a few lingered for a time in especially favorable situations. The ancient groups of insects were almost exterminated; and the stegocephalians were unable to adapt themselves to the increasing cold and the destruction of the swamps that were their habitat. A few of them survived into the beginning of the new era, only to give way to the swarm of reptiles that took their places.

But if the Permian was a time of stress, under which many of the older stocks succumbed, it was also a time of opportunity and of very rapid evolution among more progressive and adaptable types of organisms. In the Southern Hemisphere, a flora of *seed ferns* with narrow, straplike leaves (Glossopteris) had arisen, which was better fitted to withstand cold and drought than the plants of the coal forests. Spreading northward, it replaced the vanishing Paleozoic vegetation in most parts of the Northern Hemisphere. One of the chief factors in its success seems to have been the possession of seeds. A seed plant has a considerable advantage over a spore-producing plant in times when climates are strongly seasonal, for the protected embryo can get its start from the parent plant, can pass through unfavorable seasons in a resting state, and is ready for rapid growth as soon as conditions are propitious.

The *reptiles* were also among the groups that profited by the changed conditions of the Permian, for the three basic inventions described above fitted them for life among arid surroundings. The *cotylosaurs* prospered and began to split into different stocks. One of these was a very bizarre group of animals, the ship lizards (pelycosaurs), so called because the dorsal spines of the vertebrae lengthened out into tall, mastlike projections that supported a high frill of skin along the back. The name is especially appropriate for some of the later members of the group, in which projections were formed from the sides of the spines, suggesting the spars on the masts of a square-rigged ship. This stock did not long endure; but features in their skulls suggest that they stood not far from the line from which the early mammals arose, as we shall describe further on

CHAPTER XXIX

Mesozoic Life: The Age of Reptiles

With the Appalachian revolution and the accompanying transformation in life, the Paleozoic era was brought to a close. Earth history now passed into its medieval phase, the Mesozoic era, during which there may be traced the origin and development of all the truly modern groups of organisms.

During the first period of the Mesozoic, the *Triassic*, arid climates continued, but with return of mild temperatures. Most of the area of the continents was out of water, and, indeed, so far as North America is concerned, the sea never again returned to the interior of the eastern half of the continent after Carboniferous times. The lofty Appalachian range was undergoing rapid erosion all through the Triassic, and by the succeeding period, the *Jurassic*, was reduced to low elevations. The whole of the Jurassic was a time of relatively low, moist lands and mild climates, though it ended with mountain-making and a great burst of volcanic activity in western North America. The *Cretaceous* period was long and quiet; the Appalachian Mountains had been worn down to a nearly level plain, and in all the continents, there was a return of wide interior seas, which, in North America, were confined to the region west of the Mississippi. In many regions, these seas were clear and warm; the lime-secreting protozoa occurred in profusion, and their remains accumulated as thick layers of chalk, such as form the white cliffs of southern England and the chalk beds of Kansas. It is these chalk deposits (Latin, *creta*) that give the name *Cretaceous* to the period.

Sedimentary beds deposited in lakes, swamps, and land deltas are more important as a source of fossils in the Mesozoic and Cenozoic than in the Paleozoic, both because these times are closer to the present, so that more such local deposits have been preserved, and because the life of the lands was becoming more abundant and more likely to leave traces of its presence in such continental deposits.

The Marine Life of the Mesozoic Era. As has been already stated, most of the characteristic Paleozoic groups were replaced by others during the Permian. The corals of the Mesozoic seas belonged mostly to the modern Zoantharia, the Paleozoic types having disappeared. The sea lilies, sea urchins, and starfishes had been modernized. The sea urchins reached the climax of their development in the Cretaceous and the first periods of the Cenozoic. The Mesozoic brachiopods were far fewer than in the Paleozoic and were mostly of different families. The snails and bivalve mollusks increased to a wonderful extent and have been dominant groups ever since. The trilobites and eurypterids were gone, but all the more modern groups of Crustacea are represented in the Mesozoic rocks. Fish of the ancient shark and "ganoid" types continued to be numerous in the early Mesozoic; but the modern ray-finned teleost fishes developed from the ray finned "ganoids" during the Jurassic, and since Cretaceous times this has been the dominant group of fishes. The ruling marine invertebrates of this era were the ammonites, described below; and the numerous kinds of marine reptiles are discussed in our account of the evolution of the reptiles.

The *ammonites* are a group of cephalopod mollusks that flourished greatly during the Mesozoic era. They had a shell that was typically coiled in one plane, like a watch spring or like the shells of some snails. Unlike the body of a snail, however, that of an ammonite did not fill the entire shell but only the outer end. As the animal grew larger, it moved forward at intervals, secreting a limy partition back of its body and adding to the lip of the shell. The shells of older individuals thus came to be chambered, with the body of the animal in the outermost and largest chamber and its head and "arms" protruding. There is nothing on the outside of the shell to indicate the position or shape of the partitions; but if the shell is ground away until the edges of the partitions become visible, these are found to show a highly characteristic and often very complicated system of folds at their juncture (the *suture line*) with the walls of the shell. The shape of the shell, its external ornamentation of grooves or bumps, and, above all, the nature of the *suture pattern,* enable us to trace relationships in this group of mollusks with considerable certainty. The ammonites and their ancestors are abundant as fossils, and their evolutionary history has been worked out in great detail; it is unfortunate that the limitations of this study permit us to give only a brief resume of this history.

All the cephalopods, including the ammonites and their modern relatives the squids, octopus, and Nautilus, have descended from early Paleozoic ancestors that had long, straight, narrowly conical shells with simple partitions and "straight" (in reality, circular) sutures. Such shells first appeared in the late Cambrian; they became numerous in Ordovician and Silurian times and from then on declined gradually until they disappeared about the end of the Paleozoic era Coiled types with simply bent sutures appeared during the early Paleozoic and, as the nautiloids, have survived until the present. In another coiled line that began during the late Paleozoic, the sutures first became wavy (*goniatites*) and finally complex, giving rise to the ammonites. In still a third group the primitive straight shell became reduced and buried in the body; from this stock came the squids and the octopus, the shell having altogether disappeared in the latter.

The climax of ammonite evolution, so far as variety is concerned, was reached in the Triassic, from which over 2,600 species have been described; among these are found the most diverse modifications in shell form, sculpture, mode of coiling, and suture pattern. For some unknown reason, all the ammonites except those of a single line disappeared at the close of the Triassic; but from this surviving stock, there developed a new profusion of types in the Jurassic and Cretaceous. Nearly 3,000 different kinds of ammonites are known from the Jurassic alone, and some of the giants of this period had shells 5 feet, a few 10 feet across. The group remained dominant in the seas until the end of the Cretaceous period, and then for some unknown reason wholly disappeared.

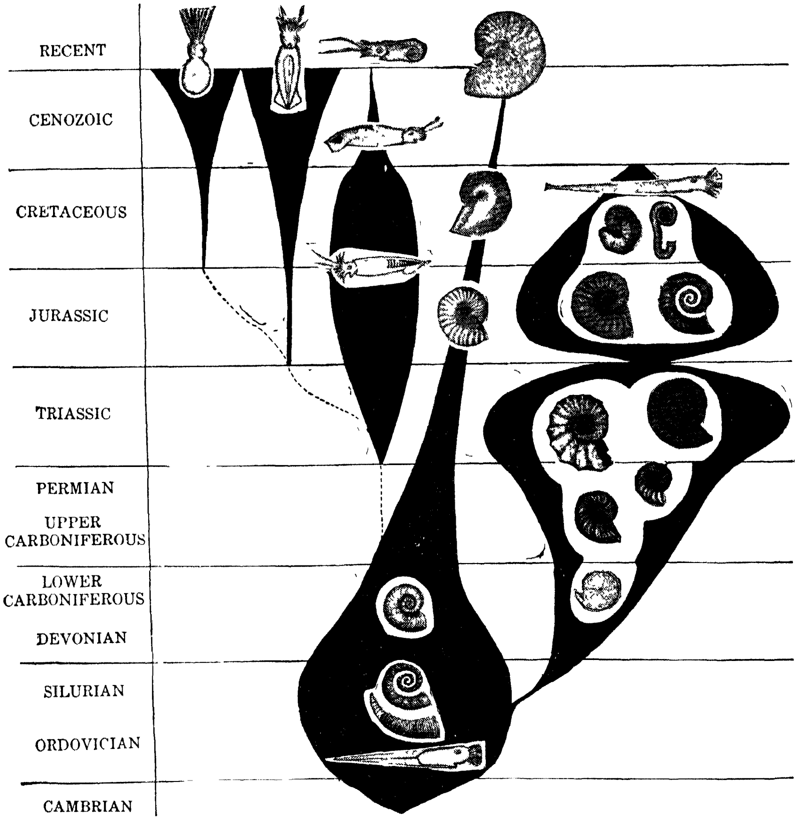

FIG. 128. *Diagram showing the relationships, relative abundance, and geological history of the main groups of Cephalopoda. Octopods and squids on left, the primitive stock and nautiloids in center, goniatites and ammonites on right.* (*From Berry, Paleontology.*)

The Land Life of the Mesozoic. The Glossopteris flora that replaced the plants of the coal swamps was composed largely of seed ferns, which were better fitted to endure the continued aridity of the Triassic than the older groups. Somehow, quite possibly from this seed-fern group, there arose *cycads*, which, with *conifers*, dominated the plant world. There were no grasslands or herbage-filled meadows, for the angiosperms did not become prominent until the Cretaceous, and grasses and the herbaceous types of plants are apparently Cenozoic innovations.

The Mesozoic forests probably contained nearly as many insects as those of today, for the *modern insect orders* came into existence either during the Permian or the early Mesozoic (with the probable exception of the butterflies and moths and a few of the lesser orders). But the greatest and most striking event in the Mesozoic world was the deployment of the reptiles, which we have now to describe.

THE EVOLUTION OF THE REPTILES

It will be recalled that the Permian cotylosaurs, the ancestral reptiles, had skulls like those of the stegocephalians, completely roofed over with bony plates, except for the eye openings. During the Permian and Triassic periods, a number of different reptile stocks developed from cotylosaurs, most of which differed from the cotylosaurs in having a *single or double opening back of the eye socket* on either side of the skull. Since the presence or absence of these openings, and their position, are important in enabling us to recognize the major stocks of reptiles, we may devote a little consideration to the way in which they arose.

The skulls of stegocephalians and cotylosaurs were big and broad, but it should not be supposed that all the space within the skull was occupied by the brain; this was small and lay beneath the center of the roof of the skull, enclosed in a narrow bony box. On either side of the brain case were muscles, largely those of the jaw, attached to the undersurfaces of the plates roofing the skull. These plates formed three series back of the eyes—a *median row*, two *marginal rows* above the back part of the mouth, and a pair of *lateral rows* between the median and marginal ones. The pull of the jaw muscles on these plates was inward and downward. If the bones were to give under this stress, it would naturally be their edges that would be pulled in, since they were not firmly fused together. If they were pulled apart along the suture between the median and lateral rows, a pair of *dorsal openings* would be formed in the temporal region of the skull; if along the suture between the laterals and the marginals, a pair of *lateral openings* would result; or if they gave along both lines of weakness, both lateral and dorsal openings would be formed (see Fig. 129). All these things actually happened.

Here is merely one example of the fact continually impressed upon us by the paleontological record, that much evolutionary change appears to take place as a response to functional requirements. Viewing only the results of evolution, we see structures and organs slowly adapting themselves to changing needs—responding to stress, enlarging with use, or dwindling with disuse. Many paleontologists are frank to attribute such evolution to the actual inheritance of the effects of use and disuse—the Lamarckian concept; but although this would seem like an easy explanation, it is really not an adequate one, for there is no acceptable evidence that the effects of use and disuse can have any effect upon heredity. We are left faced with the apparent alternatives of natural selection or of some internal guiding agency; few biologists are willing to accept the latter, since it appears inexplicable, yet it is difficult to understand how selection can account for such slow and gradual changes as have marked the evolution of most adaptive structures.

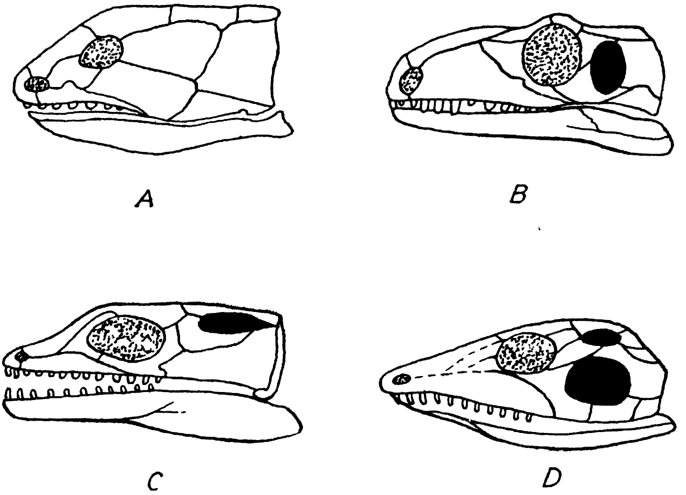

FIG. 129. *Diagrams to illustrate skull structure in the five main groups of reptiles. (A) Without temporal openings, the Cotylosaurs and Turtles (Anapsida); (B) with a lateral opening, the Ship-lizards and Mammal-like reptiles (Synapsida); (C) with a dorsal opening, the Ichthyosaurs (Parapsida) and Plesiosaurs (Synaptosauria); (D) with both dorsal and lateral openings, the Lizards, Snakes, Tuateras and Archosaurs (Diapsida). (Redrawn from Raymond, Prehistoric Life, by permission of the President and Fellows of Harvard College.)*

The Five Major Reptilian Stocks. On the basis of the structure of the skull, we can recognize five major stocks of reptiles, all of which originated in the late Paleozoic or early Mesozoic. These are briefly discussed below, after which we shall consider in greater detail the history of a few selected reptile groups that have played an important part in the history of life.

1. *Reptiles without Temporal Openings in the Skull (Anapsida).* This group includes the ancient *cotylosaurs,* and their somewhat modified descendants, the *turtles.* The turtles form a bizarre reptilian type, with one of the most remarkable armors ever developed by an air-breathing vertebrate. This armor consists of skin scales fused to the broadened

ribs and sternum. The turtles apparently originated during the Permian; by Cretaceous times, some of them had returned to the sea and lost a part of their armor. Our modern sea turtles appear to be descendants of the marine Cretaceous turtles. The land and fresh-water members of the group are still numerous and fairly successful. They are the most primitive of surviving reptiles, preserving the sprawling leg position and the unperforated skull of the cotylosaurs.

2. *Reptiles with a Pair of Lateral Temporal Openings in the Skull* (*Synapsida*). These reptiles are all extinct but are of great interest because they are on the ancestral line of the mammals. The earliest forms were the *ship lizards* (*pelycosaurs*) that lived alongside the cotylosaurs in the late Paleozoic swamps. Probably derived from the same ancestral stock as the ship lizards were the *mammallike reptiles* (*therapsids*) of the Triassic, from which mammals arose; these will be discussed in connection with the history of the mammals.

3, 4. *Reptiles with a Pair of Dorsal Temporal Openings in the Skull* (*Parapsida and Synaptosauria*). Here we find two remarkable groups of marine reptiles, both apparently developed from cotylosaur ancestors that went back to the sea in late Paleozoic times. When we first encounter them in the Mesozoic, they had already developed very complete adaptations to aquatic existence, equal to or surpassing those developed by any other air-breathing vertebrates.

The *ichthyosaurs*, or fish lizards (Parapsida), possessed as perfectly streamlined a body as any fish or porpoise—deep, narrow, and spindle-shaped. The neck was very short, as in the whales and porpoises; the tail was long and fishlike, but the tail vertebrae were bent down into its lower lobe, instead of being turned upward, as in the primitive fishes; and along the back, a cartilaginous stabilizing fin like the dorsal fin of a fish was developed. The ichthyosaurs were evidently completely marine. They did not even need to come ashore for breeding, as the sea turtles must, for they had become ovoviparous, instead of oviparous like most reptiles. This has been learned by finding the skeletons of young within the abdominal cavities of some of the fossils. The earliest ichthyosaurs are known from the Triassic, and although the group reached its climax in the Jurassic, it persisted into the Cretaceous.

The *plesiosaurs* (Synaptosauria) have been said to resemble the body of a turtle strung on that of a snake. They had a broad, flattened trunk plated with bony armor; the forelegs and hind legs were modified into powerful swimming paddles. There were two main types—one with a long, slender neck and relatively short head, the other with a shorter neck and a large head, often provided with a beak. Remains found within their skeletons prove that they preyed upon fish, ammonites, and other swimming animals, which they swallowed whole; they also swallowed gravel and pebbles to aid in breaking up the food. Plesiosaurs first appeared in the Triassic, and remained common until the end of the Cretaceous. Small ones were from 8 to 10 feet long, the largest, as much as 50 feet.

5. *Reptiles with Both Dorsal and Lateral Pairs of Temporal Openings in the Skull* (*Diapsida*). These descendants of the cotylosaurs branched out into many stocks, the history of some of which we shall trace in detail. This group, the largest among the reptiles, includes the lizards and snakes, the "living fossil" Sphenodon, and the great group of *archosaurs.* The latter were the ruling reptiles of the Mesozoic—the dinosaurs, pterosaurs, and other types. The only surviving archosaurs are the crocodiles and alligators, but the birds are believed to have descended from archosaur ancestors.

The Lizards and Their Allies. These represent a relatively unprogressive stock, which has in large measure retained the sprawling gait of the primitive cotylosaurs. However, many are swift-footed, and some run on their hind legs. They are mostly land dwellers, although a few have become aquatic. From the lizards, there came two important offshoots.

1. *The Mosasaurs.* These were huge marine lizards, some of which attained a length of 40 feet. They had a long, powerful, flattened swimming tail; the limbs were short and were modified into paddles; the mouth was immense, with numerous sharp, conical recurved teeth, the nature of which indicates that the mosasaurs were probably fish feeders. These creatures were numerous in the Cretaceous seas but became extinct before the end of that period.

2. *The Snakes.* Essentially these are elongated lizards which have lost nearly all traces of legs. They have adopted a peculiar wormlike mode of progression and have the attachments of the lower jaw modified so that large prey may be swallowed without chewing. The group is first known from the Cretaceous and has apparently been a successful one.

Tuataras, or Three-eyed Lizards. This is a group of very primitive reptiles, which we mention here only because a single species (Sphenodon) survives today (on the verge of extinction) in New Zealand, where it has been able to persist through isolation. These reptiles preserve a number of features found in the ancient cotylosaurs—in particular a rudimentary third eye in the middle of the forehead (homologous with the pineal body of higher animals).

THE HISTORY OF THE ARCHOSAURS

One of the most dramatic stories of the evolutionary record is that of the archosaurs, which, from simple beginnings in the Permian, came to dominate the lands, the seas, and even the air during the course of the Mesozoic, only to become extinct with apparent abruptness at the close of the era. We shall trace the main events of this history in the paragraphs that follow.

The Development of Bipedal Locomotion. As we have noted, the ancestral cotylosaurs had short, clumsy lateral legs and a slow, waddling walk. A number of the five main lines of reptile development mentioned above improved upon this original mode of progression, but the problem was solved most successfully by the archosaurs. The earliest members of this group were not unlike some modern lizards in form. The front legs were short; the hind legs long and much modified; the tail was massive and the pelvic girdle strong; the legs had been brought beneath the body. While resting or walking, all four feet touched the ground, but speed was attained by raising the fore part of the body, balancing at the hips by the long tail, and running on the hind legs alone.

From such a stem form, there developed a number of lines of archosaurs, some of which remained bipedal; others reverted to the quadrupedal type of locomotion but continued to show their bipedal ancestry in the structure of the pelvis and in the relatively short front legs. Those that continued as bipeds had a pair of front legs that had lost much of their original usefulness. In some instances, these legs became much reduced, almost vestigial; but in other groups, they took on changed functions and were greatly modified in form, becoming grasping hands or developing a spikelike thumb as a defensive weapon or becoming more radically altered into wings. The important lines of development of the archosaur stock are as follows:

The Phytosaurs. These were primitive archosaurs, which returned to the water. They were alligatorlike in form but had long, slender jaws and nostrils situated far back on the skull, at the base of the eyes. They were common during the Triassic but were replaced during the Jurassic by true crocodiles and alligators.

The Crocodiles and Alligators. Although these resemble the phytosaurs that they replaced, they had a different origin. Their chief structural improvement over the phytosaurs lies in the bony palate that they developed, cutting off the roof of the mouth to form an air passage extending from the nostrils at the tip of the snout to the gullet. This enabled them to breathe even with the mouth open under water, so long as the nostrils were above the surface. The group first appeared in the Jurassic and survives today as the only remaining group of archosaurs. Certain members of this stock are the only archosaurs that ever took to the sea—the marine crocodiles of the Jurassic, in which the limbs were reduced to paddles and the tail became fishlike.

The Flying Reptiles (Pterosaurs). Twice in the history of the archosaurs, the freed front legs were modified into wings—once by the ancestors of the birds, as will be seen later; again, and for the time more

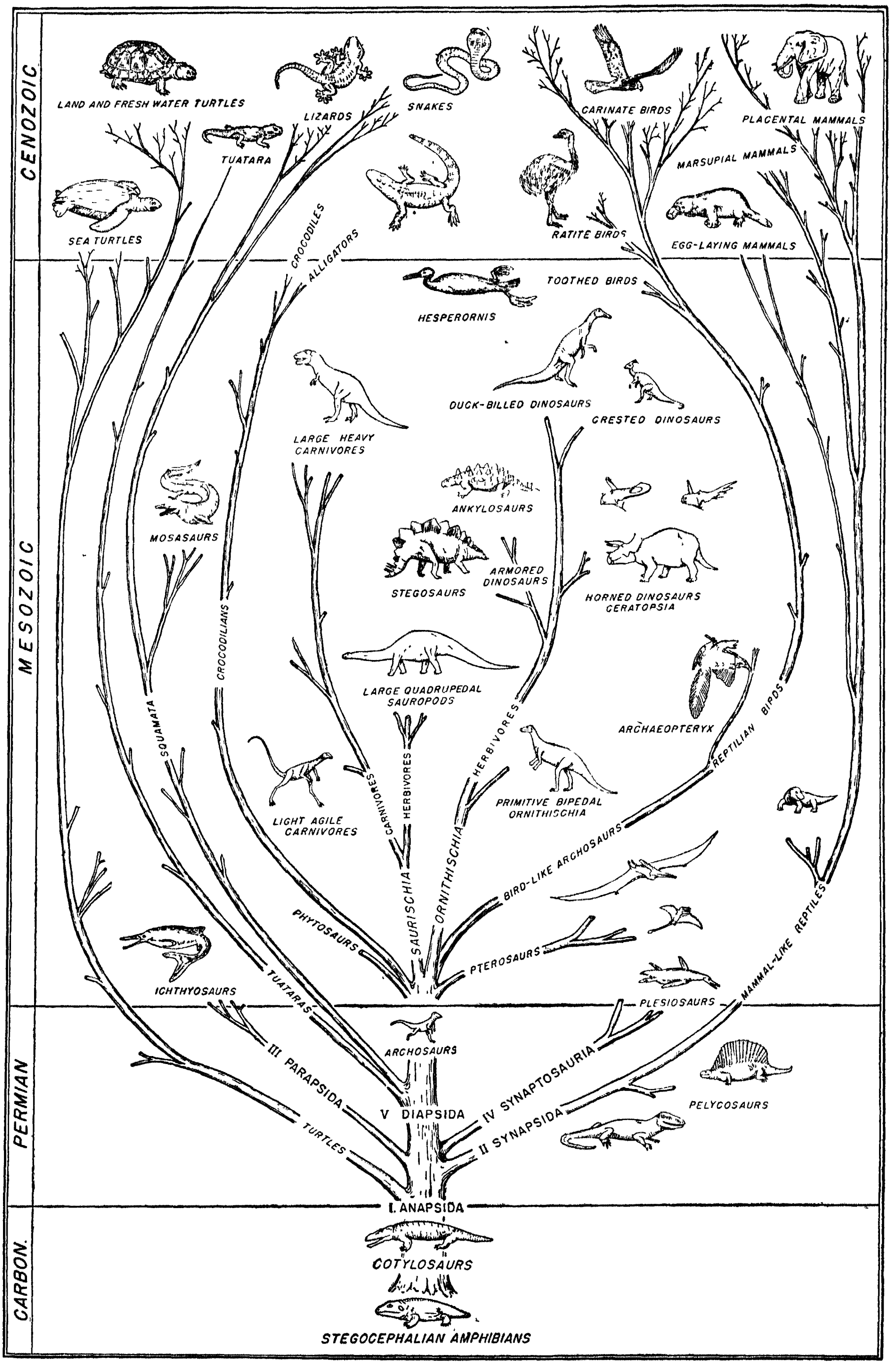
CENOZOIC
MESOZOIC
PERMIAN
CARBON.
LAND AND FRESH WATER TURTLES
LIZARDS
SNAKES
CARINATE BIRDS
PLACENTAL MAMMALS
TUATARA
MARSUPIAL MAMMALS
SEA TURTLES
CROCODILES
ALLIGATORS
RATITE BIRDS
EGG-LAYING MAMMALS
TOOTHED BIRDS
HESPERORNIS
DUCK-BILLED DINOSAURS
CRESTED DINOSAURS
LARGE HEAVY CARNIVORES
ANKYLOSAURS
MOSASAURS
ARMORED DINOSAURS
STEGOSAURS
HORNED DINOSAURS CERATOPSIA
CROCODILIANS
LARGE QUADRUPEDAL SAUROPODS
SQUAMATA
ARCHAEOPTERYX
REPTILIAN BIRDS
HERBIVORES
PRIMITIVE BIPEDAL ORNITHISCHIA
LIGHT AGILE CARNIVORES
CARNIVORES
HERBIVORES
BIRD-LIKE ARCHOSAURS
SAURISCHIA
ORNITHISCHIA
PHYTOSAURS
PTEROSAURS
MAMMAL-LIKE REPTILES
ICHTHYOSAURS
TUATARAS
PLESIOSAURS
ARCHOSAURS
III PARAPSIDA
IV SYNAPTOSAURIA
PELYCOSAURS
V DIAPSIDA
TURTLES
II SYNAPSIDA
I. ANAPSIDA
COTYLOSAURS
STEGOCEPHALIAN AMPHIBIANS

FIG. 130. *Diagram of the evolution of the reptiles, birds, and mammals.*

successfully, by the pterosaurs. These flying reptiles varied from the size of sparrows to the largest flying animal that has ever existed, the cretaceous Pteranodon, which had a wing spread of 27 feet.

The *wing* of the pterosaurs was constructed unlike that of any other flying animal, though, like those of the bird and bat, it was based on the pentadactyl limb. The first three fingers of the hand were short and clawed; the fourth finger was greatly elongated and strengthened and formed the front margin and sole support of the batlike membranous wing (without scales or feathers) that extended to the thigh; the fifth finger was lost. The bones were hollow and were filled with air, as in modern birds (though this must have been developed independently in the two groups), and the entire structure of the body was lighter than that of any bird.

Two main types of pterosaurs are known, one with a long, rigid, rudderlike tail having an expansion at the tip, the other tailless. The first disappeared at the end of the Jurassic; the other appeared during the Jurassic and attained great size in the Cretaceous. Absence of a strong breastbone for the attachment of large flying muscles indicates soaring rather than flapping flight; the nature of jaw and teeth indicate a carnivorous (probably fish) diet; and great powers of flight are shown by the occurrence of pterosaur remains in rocks formed hundreds of miles from the ancient shores. It has been suggested that pterosaurs may have roosted on cliffs like bats.

THE DINOSAURS

Of all extinct animals, the dinosaurs are those best known to the public, because the great size and peculiar forms of some of them appeal strongly to our imagination. But the group was a highly varied and successful one and included many kinds—some the largest animals that ever walked and others no larger than chickens. Two main stocks existed among the dinosaurs, each of which gave rise to a number of remarkable types.

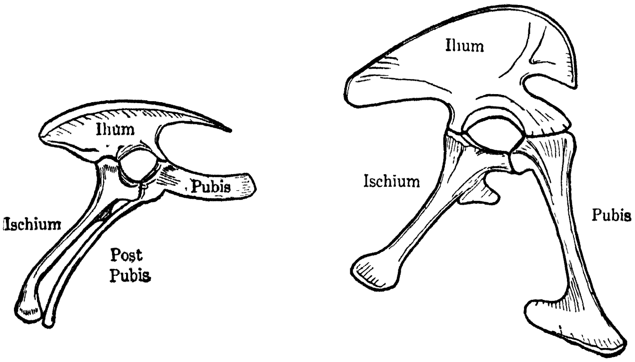

FIG. 131. *Comparison of the structure of the pelvis in the two dinosaur stocks. Left, an ornithischian; right, a saurischian.* (*From Berry, Paleontology.*)

The Two Dinosaur Stocks. The hipbones of any land animal consist of three parts. Above the socket for the thighbone is the *ileum,* fused to the backbone. Below the socket lie the *pubis* in front and the *ischium* behind. In primitive land dwellers, these two last form a solid plate, but in the early archosaurs they diverge considerably, the pubis slanting down in front, the ischium projecting down and backward, making a three-pronged pelvis. This is the structure retained by the members of the first great group of dinosaurs, the Saurischia.

In the other great group, the Ornithischia, the pubis swung backward until it lay along the lower margin of the ischium, as in modern birds; but as a support to the belly, a new bony process had grown forward from the front edge of the base of the pubis, giving a characteristic four-pronged type of pelvis. This is only the most conspicuous of a number of anatomical differences between the stocks.

The Saurischia

The Carnivorous Dinosaurs (Bipedal Saurischia). This group, abundant in the Triassic, was then mostly represented by small, swift-running types, rather lightly built. One line lost the claws of the fore-legs, the fingers became grasping organs, and the teeth disappeared. It has been conjectured that this group fed upon the eggs of other dinosaurs. The main stock grew increasingly large and culminated in the enormous Tyranosaurus of the Cretaceous—the largest carnivore that ever ruled the lands. This beast stood 19 feet high, had a skull 4 feet long, and is estimated to have weighed approximately 10 tons. Its powerful armament of teeth and the great claws of its three-toed hind feet were obviously adapted for attacking large, thick-skinned or armored prey—doubtless the large Cretaceous ornithischian dinosaurs.

The Amphibious Dinosaurs (Quadrupedal Saurischia). The dinosaurs of this stock were plant feeders, whose only protection against the attacks of the carnivorous types seems to have been bulk and weight. The line started in the Triassic, reached its maximum in the Jurassic, and had largely died out by the Cretaceous. It included the largest land animals that have ever lived. Diplodocus was a relatively slender type, with an extremely long tail, giving the whole animal a length up to 90 feet. Brontosaurus was the largest American form, shorter but heavier than Diplodocus. Brachiosaurus, the greatest of all, lived in South Africa, and reached an estimated weight of 50 tons, being further unusual in having the front legs longer than the hind ones.

The structural features of these dinosaurs are marvels of mechanical efficiency. The legs are massive columns adapted for the support of great weight; the spinal column is composed of great vertebrae, so hollowed and perforated as to give the maximum strength for the weight of material; and the entire skeleton is built on the lines of a double-piered cantilever bridge. Even so, it is thought that such great creatures must have been clumsy on land, and there is reason to believe that they were inhabitants of swamps and streams, where their weight was partly water-borne.

The Ornithischia

Primitive Herbivorous Bipeds (Bipedal Ornithischia). These Triassic forms were the ancestors of the remaining groups and already showed the following features that characterized all their descendants: loss of the front teeth and the development of a horny beak, the back teeth changing from the pointed carnivorous type to leaflike blades with rough edges and becoming more numerous. These are adaptations to a change from carnivorous to vegetarian diet.

The Duck-billed Dinosaurs (Bipedal Ornithischia). This was a group of birdlike forms, which had broad, ducklike beaks and webbed feet, and were probably amphibious. Some of them had immense numbers of teeth—as many as 2,000 in the mouth at one time—and replacements as they wore out. Some became crested by a swelling of the bones above the nostrils. This group was characteristic of the Cretaceous.

The Armored Dinosaurs (Quadrupedal Ornithischia). These were slow-moving herbivorous dinosaurs that slumped back to the four-footed method of walking. The best known types are Stegosaurus, with a tiny head, a great double row of vertical plates along the backbone, and a spiked defensive tail, and Ankylosaurus, an animated tank, with depressed body covered with heavy armor and rows of lateral spines. The members of this group are nearly all Jurassic.

The Horned Dinosaurs (Quadrupedal Ornithischia). The dinosaurs of this line possessed an enormous skull having a bony neck frill or shield, and armed on the nose or above the eyes or in both places with strong horns. The entire evolution of this stock took place in the Cretaceous, from small ancestral types without horns to the great Triceratops and other heavily armed end types. All these were plant feeders, with a horny, turtlelike beak; the armament was purely defensive.

THE END OF THE AGE OF REPTILES

Not less than 25 main orders of reptiles originated during the Mesozoic. Some of these were short-lived; but many of the archosaur groups attained great abundance and lasted a long time. Of the entire reptile dynasty, only four main stocks and one greatly reduced remnant (tuatara) are known to have lasted over the transition from the Mesozoic to the Cenozoic. The causes of this extinction are not certainly known but are probably to be sought in the renewed elevation of the continents, increased aridity, and reduction in abundant, easily obtained food necessary for sustaining the herbivorous dinosaurs; with dwindling of the herbivorous stocks, there followed of necessity a corresponding reduction in the carnivorous groups of reptiles. Whatever the cause, the reptiles lost their preeminence, and this was accompanied by a tremendous increase in the mammals and birds.

THE HISTORY OF THE BIRDS

The Oldest Known Birds. During the Jurassic period, there were shallow, quiet lagoons in what is now Bavaria, in which accumulated thick deposits of a very fine-grained limy mud, now hardened into stone used in lithographic printing. In quarries of this stone, many very perfectly preserved fossils have been found, including specimens of ichthyosaurs, pterosaurs, and other marine or aerial animals. Here were also found the oldest fossils of birds, with even the outlines of the feathers preserved. The fossils are of two slightly different kinds of birds, but since they are alike in all important respects, we may refer to them simply as Archaeopteryx, the oldest name. The principal differences between these most ancient of birds and our modern types are shown in the following tabular comparison.

Archaeopteryx	*Modern Birds*
Feathers	Feathers
A bill with many sharp teeth	A toothless bill
A long, reptilelike tail with a double row of feathers	A short tail with fanlike spread of feathers
Feeble wings, with the three anterior fingers clawed and projecting from the front margin of the wings and the digits not fused together	Strong wings, the digits fused and the claws lost (except in the hoatzin)
Solid or, rather, not air-filled, bones	Hollow bones, the interior of the bones occupied by an air space, as in pterosaurs
A very weakly developed breastbone	A large breastbone, related to the great development of the flying muscles

Obviously, these first birds were hardly more than feathered archosaurs; if their feathers had not been preserved, it is doubtful if they would have been recognized as birds. They probably developed from tree-dwelling archosaurs that evolved a gliding habit, like that of modern flying squirrels.

Other characters in which modern birds differ from their archosaur ancestors are: warm blood, four-chambered heart and double circulation, great increase in development of the sight, balance, and coordination centers of the brain, incubation of the eggs, and increased complexity of behavior (including such phenomena as song, migration, social habits, etc.). It is, of course, impossible to determine how far advanced Archaeopteryx may have been in any of these respects—probably not much beyond the reptile stage.

Subsequent Evolution of the Birds. Bird fossils are rare. Two birds are known from Cretaceous time: Ichthyornis, much more like modern birds than Archaeopteryx, but still with toothed jaws and many other reptilian features; and Hesperornis, a marine creature of some size, which fed upon fish and which was far advanced in specialization, having lost not only the power of flight but all trace of the forelimb except the humerus and shoulder girdle.

Such reduction or loss of wings has occurred many times in different stocks of birds, most commonly among those which tended to develop large size (moa, ostrich, dodo, etc.) or which became aquatic (Hesperornis, penguin, etc.). The extent of reduction varies from that just sufficient to prevent sustained flight to complete loss of external trace of the forelimb. In some instances, the reduced forelimb has taken on new functions (paddle, as in penguin; sails increasing speed in running, as in ostrich); in other birds, the wings are completely useless, rudimentary structures, the presence of which is understandable only as the result of descent from fully winged ancestors.

Most of the modern families of birds had already evolved by the early Cenozoic, and the birds have been second only to the mammals in dominating that era. They appear to have suffered less than the mammals during the Pleistocene glacial periods and show no signs of being on the wane, as do many mammal stocks.

CHAPTER XXX

Cenozoic Life: The Age of Mammals

The history of the Cenozoic leads by gradual steps to the present order of things, though climatically there were violent breaks in continuity. Never during the Cenozoic were there extensive transgressions of the sea into the interiors of the continents. In many parts of the world, great ranges of mountains were formed; the Alps, Himalayas, and others are of Cenozoic age. In North America, the Rocky Mountains had been uplifted earlier; during the early Cenozoic they were gradually destroyed, until in the Oligocene the interior of the continent was a vast, gently rolling lowland, with here and there low ranges of hills, the remnants of the Mesozoic mountains. With the Miocene, the whole of western North America began to rise; the Sierra Nevada and a newer generation of Rockies have been in process of uplift ever since, and the rise of these caused the formation of the Great Basin deserts and the aridity of the Great Plains.

During the late Eocene and Oligocene, climates were mild, and there seem to have been great forests over much of the country, made up prevailingly of modern plants but differing from those of today in that warm-climate types of vegetation extended far beyond their present northern limits. At the periods of maximum warmth, palms and breadfruit trees occurred in Colorado and Wyoming, where their leaves are found preserved in the sediments of the ancient lakes around the shores of which they grew.

With the Miocene uplift, a change of climate set in, with increasing aridity and spread of grasslands at the expense of the forests. This was the period of maximum development of the mammals. All through the Pliocene, there was continued uplift, with progressive cooling and drying of the climate. In the latest geologic period, the Pleistocene, came the series of ice ages, which are scarcely more than past. The Pleistocene glaciations had a tremendous effect upon the life of the world. Many types of mammals became extinct at this time, our modern mammal faunas being mere remnants of the pre-Pleistocene ones.

THE HISTORY OF THE MAMMALS

Like the birds, the mammals arose from a reptilian ancestral stock. We shall have to go back to the close of the Paleozoic and the early Mesozoic to see the start of the mammal line, and it will be necessary to review the characteristics that distinguish the mammals in order to appreciate the changes that occurred in their evolution from reptiles.

Characteristics of Mammals. Some of the most important mammalian characteristics may be briefly described as follows:

Reproductive Features. The young of mammals are given postnatal care and are nourished by milk secreted by special *mammary glands;* in all but the most primitive mammals, the young are "born alive" (*i.e.*, mammals are *viviparous*); and in most living mammals, there is a *placenta,* a special embryonic structure developed from the reptilian allantois, by means of which the embryonic mammal lives as a parasite upon the mother until a late stage of development.

Warm Blood. The mammal has a temperature regulating mechanism, including a hairy skin covering and sweat glands; the temperature is maintained above that of the normal environment by active metabolism and active oxidation, served by rapid respiration and an efficient circulatory system based on the four-chambered heart and double circulation.

Brain. There has been great increase in brain size, mostly the result of enlargement of the cerebral hemispheres (unlike the enlargement of the brain in birds, in which it is the sight, balance, and coordinative centers that have increased most markedly); the remainder of the brain is not much changed from the reptilian condition.

Skull. The skull is very different from that of the reptiles, many of the reptile bones having been lost. The opening for the pineal eye in the top of the skull is closed; the originally solid temporal region is pierced for the accommodation of the jaw muscles, leaving a bar or arch at the edge of the cheek; the brain case is greatly swollen; the single reptilian condyle is replaced by a double condyle, where the skull is attached to the vertebral column; the nostrils open into a dorsal chamber in the roof of the mouth, cut off from the rest of the mouth cavity by a bony partition, the *palate;* the jaw is formed of a single bone (the *dentary*) instead of seven, as in the primitive reptile; and the articulation of the jaw is changed.

Teeth. Instead of the row of similar conical teeth characteristic of primitive reptiles, mammals typically have, in each row, 3 incisors, 1 canine, 4 premolars, and 3 molars—a total of 44 teeth in the entire dentition. Most mammals have lost some of this original mammalian tooth complement; man has 32 teeth remaining.

Ears. Reptiles have one small bone to transmit vibrations from the eardrum to the inner (perceptive) part of the ear; mammals have three.

One (the *stapes*) is the old reptilian earbone; the other two (*malleus* and *incus*) are part of the set of bones that originally formed the jaw hinge of the reptile, sunk in and enclosed by the parts of the outer ear. In mammals, an *ear flap* is developed, which concentrates the sound waves; and the *eardrum* is sunk into the head so that it lies at the bottom of a tube.

Locomotion. The legs of mammals are swung under the body into a fore-and-aft position, elbows back and knees forward, so that less energy is used in lifting and supporting the body and more in propelling it. The *digits* of the front and hind limbs of the reptile have the following numbers of bones (starting with the "thumb"): 2, 3, 4, 5, 3; in mammals, the number of digit bones has been reduced to: 2, 3, 3, 3, 3. The general tendency among many mammals has been to stand higher and higher on the toes, increasing the length of the propelling lever.

Metabolic Activity. Except for the birds, mammals are the most active and alert of vertebrates; all the modifications noted above are related to this increased activity. The complexity associated with these changes appears to be the main cause of the slow embryonic development and the peculiar features of mammalian reproduction.

Reptilian Ancestors. The earliest animals showing traces of mammalian characteristics are not found among the highly modified and advanced reptiles but among an offshoot from the primitive cotylosaurs —the *ship lizards,* members of the second of the five main divisions of the reptiles. It is not, however, the peculiarly modified ship lizards themselves but the ancestors of this stock that probably lie on the direct line of mammalian development. The features of the ship lizards (pelycosaurs) that indicate relationship to the early mammals are the presence of an opening in the side of the skull for the jaw muscles, and the fact that the skull is nearly closed behind. Pelycosaurs are well represented in the Red Beds of Texas, which are of Pennsylvanian and lower Permian age—a time when the cotylosaurs still flourished and the archosaur stock had not yet begun its spectacular rise.

The *Mammallike reptiles* (*therapsids*) represent a further step in the development of the mammals. They were common in the later Permian and the Triassic; most of their fossils have been found in South Africa.

Cynognathus, the dog-jawed reptile, is representative of the group. It was a rather active, carnivorous animal, reaching a maximum length of 4 or 5 feet. The skull was intermediate in type between that of a primitive reptile and a mammal; many of the bones absent in mammals were reduced in size or already lost, and the opening for the pineal eye was very small. In this and other therapsids, the bones at the angle of the jaw had become detached from the side of the head and were sunk in a depression and reduced in size (on their way to becoming earbones); the dentary was enlarged, and the remaining bones of the jaw small; the roof of the mouth was arched up, and the beginnings of the palate bone were forming beneath it (the origin of the mammalian false palate). Double occipital condyles were already present in Cynognathus. The teeth were differentiated into incisors, canines, and cheek teeth, and there is some indication that they were limited to two sets, "milk" teeth and permanent teeth. The limbs had already shifted far toward the fore-and-aft mammalian position; the digits retained the reptilian number of bones, but those destined to be lost were tiny (in some of the mammallike forms, the number had already been reduced to that of mammals). However, in spite of these mammallike characteristics, Cynognathus and its allies were still reptiles in most respects. Nothing is known as to whether they were warm-blooded, had hair or scales, or nursed their young.

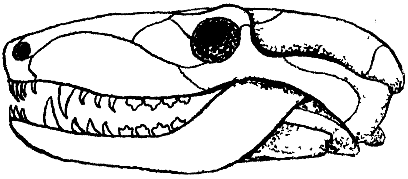

FIG. 132. *Skull of a Permian mammal-like reptile, similar to Cynognathus, showing the single dentary bone and differentiated teeth which are mammal-like characters.* (*Redrawn after Broom.*)

The Egg-laying Mammals. Two very specialized survivors of an egg-laying stock of mammals occur today in Australia, where they have been able to persist through the protection afforded by their geographic isolation and their retiring habits. These are the *duckbill* (Platypus) and the *spiny anteater* (Echidna). They have fur and nurse their young but lay shelled eggs. The chances are that most Mesozoic mammals early developed the viviparous habit and that these egg-laying types have had a long separate history apart from that of the remaining groups of mammals.

The Two Stocks of Viviparous Mammals. By late Mesozoic time, there were, in addition to several groups that have apparently left no descendants, two well-differentiated stocks of viviparous mammals. One of these, the *marsupials*, gives birth to its young in a very immature state—practically as embryos—and they are then usually protected in a skin pouch covering the region of the mammary glands, where they remain until well along in their development. The mammals of this group are in many respects more primitive than those of the other stock, the *placentals*, in which the young are retained within the body of the mother until nearly or quite ready to take care of themselves and during this time are nourished within the uterus by means of an allantoic placenta.

The Marsupials or Pouched Mammals. In addition to possessing the characteristic pouch or *marsupium*,[1] which gives the name to the group, the marsupials differ in numerous other respects from the placental mammals. Instead of there being a true uterus, the two oviducts are either entirely separate or else may show a variable degree of fusion at a point above their individual openings, forming a chamber from which a temporary third opening permits escape of the young at time of birth. The embryo, during its short period of internal development, is in some forms attached by a primitive allantoic placenta but in others either by the yolk sac or by both yolk sac and allantois. The embryonic young at birth crawl to the nipples and attach themselves; the end of the nipple swells within the mouth until it can be removed only by force, and the windpipe, or trachea, of the young animal grows up into contact with the nasal chamber, permitting breathing to go on even while milk is being swallowed. In most marsupials, there are two flattened, rodlike bones projecting forward in the abdominal wall from their attachments to the pubis; these are lacking in all placentals and seem to be remnants of the skeletal supports of the abdominal floor found in primitive reptiles.

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[1] The pouch has been reduced or lost in some marsupials; thus in the banded anteater of Australia, and some of the smaller species of South American opossums, the young hang fully exposed from the nipples.

At the present time, marsupials occur only in Australia, Tasmania, and South America, with the solitary exception of the North American opossum. They were probably numerous in the late Mesozoic and may have been widespread, although no fossils except those of opossums have been found in North America and Europe. Irrespective of where the group originated and how extensive its distribution may once have been, marsupials evidently reached Australia and South America during the Cretaceous or earlier, prior to the submergence of the land bridge between the Australian region and the Asiatic continent. At this time, the placentals either had not yet developed or at least had not reached the region of the Australasian bridge, since they never succeeded in entering Australia. In South America, the marsupials were largely overrun and supplanted by the placentals, but in Australia they have had the entire continent practically to themselves up to the coming of man and the animals introduced by him.

The ancestral type of the marsupials was apparently a small, arboreal, opossumlike animal. In the Australian region, the descendants from such an original stock, protected by their isolation from competition with the more progressive placentals, underwent an *adaptive radiation* that has become a classical illustration of this phenomenon. The widest variety of forms came into existence, including some adapted to almost every sort of habitat and mode of life. Among the modern inhabitants of the Australian region are "mice," "shrews," "squirrels," "cats," a "wolf," a wolverinelike animal (the Tasmanian devil), "moles," an "anteater," slothlike "bears," badgerlike wombats, and a variety of types like nothing else on earth, including kangaroos, bandicoots (rabbitlike animals with long tails), and the flying phalangers. All these are marsupials, though in many instances they show extraordinary superficial resemblance to the placental mammals whose names they have been given by the European settlers of the continent. Besides the living types, there were formerly present a great lionlike marsupial, giant kangaroos, and huge rodentlike forms with the bulk of a rhinoceros, all known from fossil remains. Many of the recent species are now threatened with extinction, either because their places are being taken by placental mammals introduced by man or because they are being killed by introduced predators or by man himself. The only placental mammal that was present in Australia at the time that continent was discovered by Europeans was the dingo, a wild dog that had probably been brought in by primitive man.

The Australian marsupials furnish a striking example of another evolutionary phenomenon, known as *convergent evolution.* On the one hand, we see the adaptive radiation that, as a group, they exhibit; but the other aspect of this same development is the close resemblance to other and only distantly related forms, which various members of the group have come to show. Thus the marsupial mole of Australia is almost a counterpart in appearance and habits of the placental golden mole of South Africa, the sheep-killing Tasmanian marsupial wolf of the true placental wolves of the Northern Hemisphere. These forms are of different ancestry, and the similarities are mere analogies, related to the similar modes of life and habitats of the animals showing them.

THE HISTORY OF THE PLACENTAL MAMMALS

Primitive Placentals. *The Insectivores.* The ancestral stock from which the great majority of modern mammals, including ourselves, seems to have developed was probably not unlike the modern forms that we call *shrews;* moles and hedgehogs are somewhat more specialized related types. The members of this stock were small, rather general in their food habits, with brains poorly developed by modern standards; but they had the great advantage of viviparity and of birth at a late stage of development because of having the placenta. The oldest fossils of insectivores are known from the late Cretaceous. During the Paleocene, there was rapid development of this stock along many lines, with a strong tendency toward increased size. By the Eocene proper, the main lines of mammalian development had already been established.

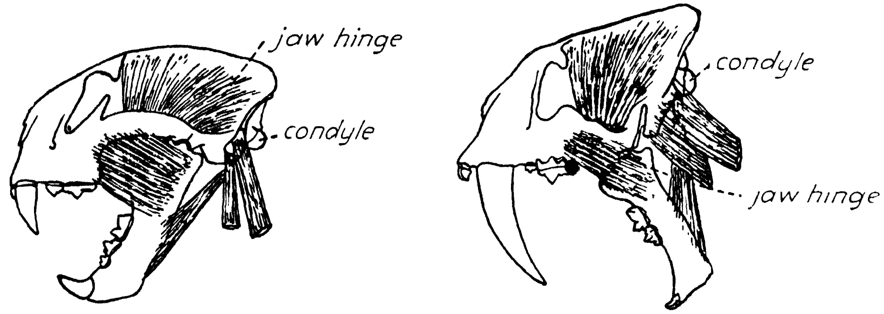
Archaic and Modern Stocks. In all the mammalian groups that arose from the insectivores, there may be noted a tendency toward increase in relative size of brain, and modification, particularly of teeth and feet, with increase in body size. In every group, we may distinguish between an earlier stage of development in these features (particularly those of the brain) and a later and more advanced stage, so that in each stock, we may speak of *archaic* and of *modern* types. Many of the archaic stocks became large and highly specialized and were very successful for a time, only to be replaced by a more modern type with better brain and greater adaptability, even though it might not be so specialized. We shall be able to follow only a few of the more important lines of development of the modern mammals.

The Carnivores. Among carnivores, the major changes have been those of the brain and teeth; the rest of the skeleton remains quite primitive, even in modern forms. The need is for cutting and holding teeth, not for chewing; the incisors are retained, the canines greatly enlarged; the molars tend to be lost and the premolars reduced to a few shearing teeth. The Eocene carnivores belong to a group called the *creodonts,* or flesh-toothed mammals. Among the creodonts, the brain was small, and the teeth were still mostly present, some of the molars or premolars being modified into shearing teeth. Some of these archaic carnivores were weasellike; others were as large as a wolf or lion. They were eventually replaced (toward the end of the Eocene and the beginning of the Oligocene) by modernized carnivores with bigger brains, the ancestral *fissipedes* ("split feet"), which gave rise to modern cats, dogs, bears, and other living types. (The sea carnivores—seals, etc.—had a different history.)

The herbivores on which the creodonts fed were, to start with, small and not very swift. Their whole history was one of increase in size and in speed, or increase in size with development of protective weapons and thick skin. Also, the early ungulates, like the early creodonts, had small brains and presumably little intelligence; they were later replaced by larger brained and hence more intelligent types, and this took place before the change in the carnivores. These two things together probably account for the downfall of the creodonts, which were neither very speedy nor very intelligent. The ancestral fissipedes, however, from which all later carnivores have developed, showed considerable advance in both these respects. *Cynodictis,* an example of this stock, is about intermediate between dogs, cats, and weasels. By the Oligocene, such types had already given place to the ancestors of each of the modern families of carnivores.

The Cats. The cats were numerous in the Oligocene. They have lost every molar; a cat cannot chew at all, though it is admirably equipped for stabbing, biting, and slicing. The cats specialized on stalking and sudden attack, not on the long chase, like the dog group. They early diverged into two divisions, the *true cats* and the *sabertooths.*

The sabertooth line is now extinct, but its members were common until the Pleistocene. The saber-toothed tiger (Smilodon) was widespread over Europe and North America; complete skeletons have been found in the La Brea tar pits in California, and a tooth in a Florida cave. Early sabertooths were not very different from true cats, but as time went on, the canine teeth gradually elongated into tremendous knifelike blades with serrate edges, fitted for stabbing and ripping; and the jaw was modified so that it could be swung back against the neck out of the way. The structure of the jaw and teeth in this group was almost certainly an adaptation for piercing the thick skins of many of the Pliocene and Pleistocene mammals—horses, rhinoceroses, ground sloths, mastodons, and elephants. The sabertooths were probably blood drinkers rather than flesh eaters. Disappearance of the group is believed to have resulted from the decimation of the large herbivores that occurred during the ice age.



Skull of biting cat (tiger) Skull of saber-tooth (Smilodon)

FIG. 133. *Comparison of the skulls of a typical biting cat and saber-tooth.* (*Redrawn after Lull, Organic Evolution, The Macmillan Company.*)

Hoofed Mammals (***Ungulates***). Several different lines of early mammals became herbivores, developed teeth fitted for grinding and chewing coarse vegetation, and underwent parallel modifications in the form of the legs and feet. For descriptive purposes, we group these as the *ungulates*, even though the resemblances between the different lines are in some instances the result of merely analogous modifications.

Evolutionary Tendencies in Ungulates. Besides the increase in size that seems to have been a regular accompaniment of specialization in terrestrial herbivorous mammals, the chief evolutionary changes in ungulates affected the teeth and legs.

Teeth. The molars and premolars became altered into ridged or flat-topped champing or grinding structures, unlike the conical or slicing type found in carnivores. In many lines of ungulates, the great wear on the grinding teeth was eventually compensated for by development of molars which grow for some time and which are high-crowned to start with.

Legs. Protection against the attacks of carnivores was attained in ungulates sometimes by the development of great size and strength (often accompanied by evolution of protective weapons) but more commonly by the attainment of speed in locomotion. The latter development has been especially characteristic of the inhabitants of grasslands and semiarid regions, where little concealment is possible and where long distances must often be covered in search of food and water. In speedy ungulates, the legs have been made rigid by modification of the joints, in a manner very efficient for straightway locomotion but very poorly adapted for any other type of movement. The humerus and femur have become short, giving a fast, powerful drive; the radius-ulna and tibia-fibula have become long, swinging fore and aft over a wide angle; and the palm and sole bones (metacarpals and metatarsals) have been much elongated, so that by running on the toes, a third functional segment is added to the leg. With further development of speed, the toes themselves have been lifted from the ground, until the animal is supported only on their tips; at the same time, the claws have become modified into short, broad, horny structures, the hoofs.

The Three Types of Ungulate Foot. Depending upon whether the animal is fitted for swift running (cursorial type) or is ponderous and slow-moving (gravigrade type), we may recognize three chief lines of modification of the legs and feet.

1. In *cursorial ungulates*, it is evident that as they rise upon their toes, there will be a tendency for the short side toes to fail to reach the ground and to cease to function. This has happened in two ways:

a. In one group, the major axis of the foot passes through the *middle toe.* With rise of the foot, the two outer toes are first lifted from the ground, become functionless and eventually rudimentary; then the next two undergo the same changes, leaving the animal, in extreme instances, perched on the tip of the middle toe. This is the case with the horse. Ungulates with the major axis of the foot passing through the middle toe are called the *odd-toed*, or Perissodactyla.

b. In another group, the major axis of the foot lies *between the third and fourth toes.* When the weight is rested equally on these and the foot is lifted, the "big," or first, toe is the first to leave the ground; then follow the second and fifth, leaving the animal resting upon the tips of two toes, the third and fourth. Ungulates of this type are called the "cloven-hoofed," or *even-toed*—the Artiodactyla.

2. In the *gravigrade ungulates*, whether they are of the perissodactyl, artiodactyl, or other stocks, support of great weight becomes the chief function of the leg, and this involves entirely different adaptations from those found among the cursorial types. The foot tends to retain all the toes, which become short and stubby; the heel rests upon a thick pad of connective tissue; the leg bones become comparatively short and massive; and the entire leg and foot are lined up into a thick, pillarlike structure. Examples of animals showing this gravigrade (weight-supporting) type of leg are the elephant and rhinoceros, among living mammals, and the

uintatheres, titanotheres, mastodons, and mammoths, among extinct forms.

HORSES, CAMELS, AND ELEPHANTS

The ungulates include a dozen or more orders of living and extinct mammals, of which the Perissodactyla and Artiodactyla are the most important. The horses belong to the first, the camels to the second of these two orders. The elephants, with the conies and sea cows, form another assemblage, the *subungulates.* Extraordinarily complete fossil records are known for these three groups, particularly for the horses and elephants. Starting in each instance with small, primitive types having feet not far removed from the primitive pentadactyl type, the horses ended as cursorial one-toed forms, the camels as cursorial two-toed forms, and the elephants as gravigrade types.[1] In each group, increase of size accompanied specialization of feet and teeth. The evolutionary records of these three groups are classical examples of the evidence of evolution afforded by paleontology. Here we can only briefly summarize their histories.

Horses. The oldest member of the horse group is *Eohippus*, from the early Eocene. It was a small creature no larger than a fox terrier (about 12 inches tall), with feet that had already undergone some modification from the primitive pentadactyl condition. There were still four toes on the front feet and three on the hind. The teeth were short-crowned, and the head was short, with the eye socket situated near the middle.

Mesohippus, of the Oligocene, had increased in height to 18 inches; both feet had three toes; the teeth were still short-crowned. *Merychippus*, of the Miocene, was 3 feet tall; the feet were still three-toed, but the two side toes did not normally touch the ground. In this horse, the milk molars were still short-crowned, but the permanent molars were becoming high-crowned, suggesting that the animal had changed to a diet of grasses and lived on the plains rather than in the forest. The facial part of the head was elongating; the eye orbit was situated farther back and was fully closed behind for the first time.

Pliohippus, of the Pliocene, was the first one-toed horse, with the second and fourth toes represented by splint bones, the first and fifth lost without trace. It was the size of a small pony (3 to 4 feet high), and the molars and premolars of both milk and permanent sets were moderately long-crowned and had grinding surfaces.

Equus, the genus to which the modern horses belong, appeared in the Pleistocene. Recent horses attain a stature of 5 feet or more; the feet

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[1] For a full and interesting account of the history of these and other groups, see Romer's excellent book *Man and the Vertebrates*, to which we are indebted for some of the information here presented.

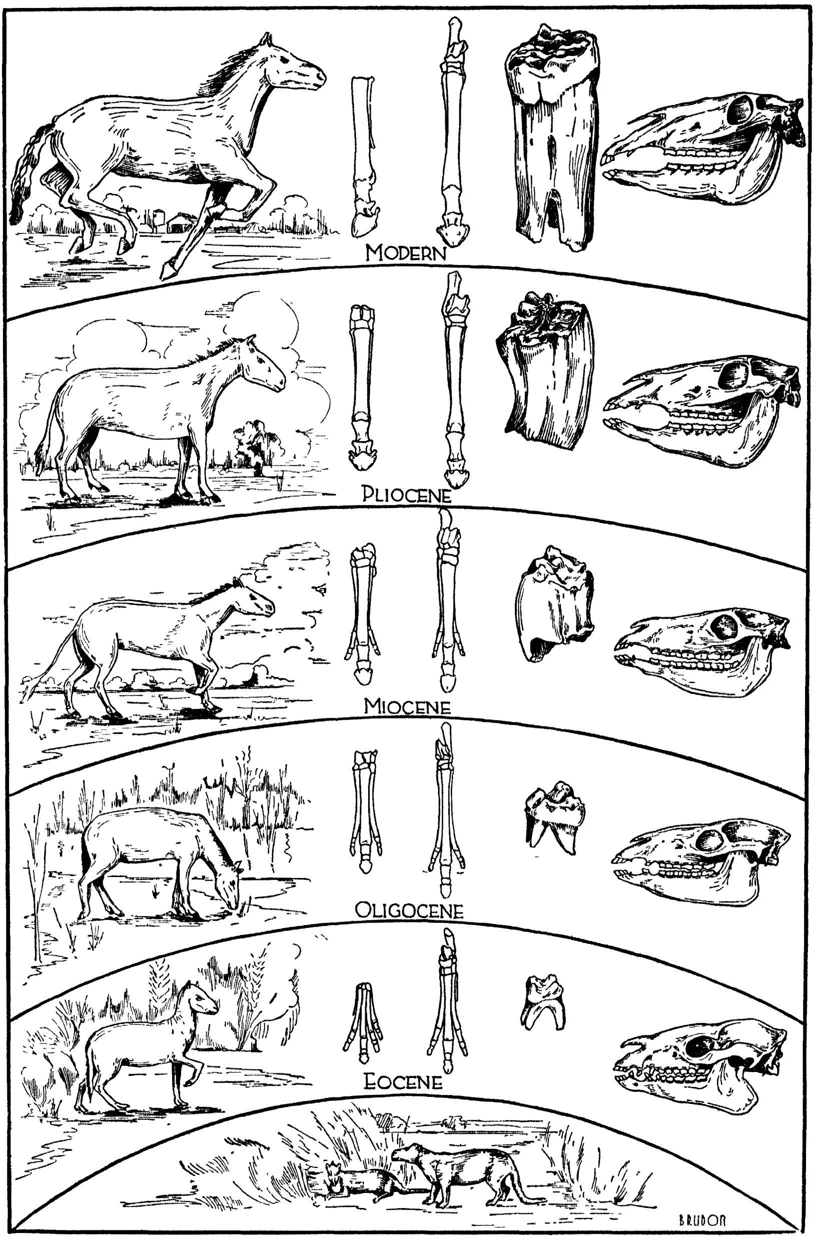

FIG. 134. *Diagram of the evolution of the horse. Lowest panel, Phenacodus, a generalized "archaic" ungulate of the Paleocene. The remaining figures are horses; from bottom to top those shown are Eohippus, Mesohippus, Merychippus, Pliohippus, and Equus, or the modern horse. Within each panel, from left to right, there is shown a reconstruction of the horse against a background of its typical environment; the fore and hind foot, showing the progressive reduction in lateral digits; one of the permanent molar teeth; and the skull. Only the teeth are drawn to scale.*

are one-toed, with splint bones representing the second and fourth toes; the teeth are very long-crowned and columnar, grow throughout early and middle life, and have a grinding surface made up of hard ridges of enamel alternating with grooves where the softer dentine and cement are exposed; the skull is very long, with the eye situated far back.

Camels. The history of the camels resembles that of the horses, though it is less complete. As in the case of the horses, most of the evolution of this group occurred in North America. The earliest known member of the camel line is *Protylopus,* of the late Eocene. It was the size of a large rabbit; there were 44 teeth in a continuous row, the molars being low-crowned; the orbit of the eye was open behind; the forefoot had 4 separate functional toes, the hind foot 2 functional and 2 reduced toes.

Through a series of stages comparable to those described in the horse lineage, we can trace the changes from this original stock to the conditions found in the modern camels, guanacos, vicunas, llamas, etc. In the modern genus *Camelus,* the size has enormously increased; the teeth are reduced in number to 34, separated into several groups by wide spaces; the molars are tall-crowned; the orbit of the eye is closed behind; the lateral bones of the palm (first, second, and fifth metacarpals and metatarsals) are lost without trace on all feet; and the two remaining toes have the bones of the palm elongated and fused into a double bone (the cannon bone).

Elephants and Mastodons. The Proboscidea (elephants and their allies) apparently originated in Africa, whence they spread to all the northern continents and eventually even to South America. The earliest member of the series is *Moeritherium,* known from the late Eocene and early Oligocene of Egypt and India. This animal was probably not the actual ancestor of the later proboscidians, but an offshoot from the ancestral line that had developed amphibious habits; it nevertheless gives us a good idea of what the earliest members of the stock were like. Moeritherium was somewhat piglike in form, standing about 3 feet high, and had a neck long enough to let the mouth reach the ground. It had lost relatively few of the 44 original mammalian teeth, its tooth formula being $I\frac{3}{2}$, $C\frac{1}{0}$, $P\frac{3}{3}$, $M\frac{3}{3} = 18$, or 36 teeth in all. Suggestions of later proboscidian developments are to be seen in the elongation of the second incisors of each jaw into short tusks, the incipient loss of the remaining incisors and canines, the arrangement of the four conical tubercles on the molar teeth into two transverse rows, the shortened facial region of the skull and its wide cheek-bones, and the shifting of the nasal openings back of the tip of the snout, perhaps indicating the presence of a prehensile upper lip but not of a proboscis. From some ancestral type not far removed from Moeritherium there evidently arose several stocks of Proboscidia, some of which led to the mastodons and elephants.

The next stage in the development of the group is represented by two closely related forms, *Palaeomastodon* and *Phiomia,* the first from the upper Eocene and the second from the Oligocene of Egypt. These types were considerably larger than Moeritherium, ranging in size from that of a tapir to that of a half-grown Indian elephant. The leg bones were already taking on the gravigrade structure; the neck was still fairly long, although the posterior neck vertebrae had commenced to shorten; the skull was higher at the back, with an increase in the spongy bone of the posterior part of the skull and more area for muscle attachment; and the nasal opening was just in front of the eyes, as in the modern tapir, suggesting the presence of a short trunk. There were four well-developed tusks representing the second incisors, but the rest of the incisors and canines were gone. The upper tusks were large, the lower ones short, directed forward, and placed at the tip of the much elongated lower jaw. The remaining twenty-two teeth were grinders, consisting of three upper and two lower premolars, and three upper and three lower molars on each side. The jaw was still long enough to permit the milk grinders to be replaced by the permanent set of grinders, which were all present in the mouth at once and were used in the ordinary way. The molars had six cusps arranged in three transverse rows.

There is, unfortunately, a gap in the recorded history of the proboscidians during the middle and upper Oligocene. During this time the group seems to have remained confined to Africa and southern Asia, but when it began its world travels in the Miocene it had already become differentiated into several distinct evolutionary lines. One such line included the very bizarre *deinotheres,* which lacked the upper tusks, and had the lower tusks and jaw curved downward and backward, apparently to form a hoe-like digging organ. These occurred in the Old World during the Miocene and Pliocene, but never reached North America. The second major division of the proboscidians included the *mastodonts*—mastodons and their allies—in which the grinding teeth were still simple, low crowned, and rooted, their grinding surfaces having a small number of transverse, enamel-covered ridges separated by deep valleys containing no cement. Such teeth are better fitted for browsing and champing succulent vegetation than for grinding harsh food. The third major group, the *elephants,* arose much later, during the late Miocene or early Pliocene, from one of the stocks of the mastodonts.

The Mastodonts. During the Miocene and Pliocene at least four major families of mastodonts came into existence. Members of all of these lines sooner or later reached North America, where at least a score of types have been found. The best known of these is the Pleistocene and postglacial American mastodon, *Mastodon americanus,* which was common over most of the United States. It was a member of the *true mastodons.* This stock, like all the other mastodonts, began with long-jawed types; but in this line the lower jaw soon lost its tusks and began to shorten, while the upper tusks and trunk elongated. The teeth (Fig. 117) remained of the primitive mastodont pattern, low crowned and rooted. Being much smaller than elephant teeth, there was room for as many as three grinding teeth at a time on each side of each jaw, though the usual number in use at one time was two. In these, as in the other mastodonts, the teeth were cut vertically in the normal manner for mammals, instead of coming in obliquely from behind as in the elephants. The latter were probably derived from certain members of this family, as is noted below.

The other three mastodont families included a much more diversified assemblage of types. In some of them the originally elongate jaw became tremendously lengthened; in the *four-tusked mastodons* it bore short conical tusks whose tips were nearly even with the ends of the large upper tusks; in the *shovel tuskers* the upper tusks were lost, and the lower ones, borne by the overdeveloped jaw, became broad and spade-like digging blades; in the *shovel-jawed mastodons* both sets of tusks were lost, and the end of the long jaw itself formed a thin-edged shovel-like organ probably used for digging in mud. In many of the less peculiar lines of development short-jawed types with long upper tusks were eventually produced in a manner parallel to that seen in the true mastodons.

The Elephants. The stock of true mastodons from which the elephants developed is apparently represented by *Stegodon,* from the Pliocene of India. This is definitely a transitional type between the mastodonts and the elephants. It had large upper tusks, a short lower jaw, and a relatively high, short skull, with an increased amount of spongy bone at the rear. The teeth have more numerous ridges than those of the mastodonts, and the valleys have a deposit of cement over the enamel, though it does not fill the valleys as it does in the elephants. The further changes necessary to produce the characteristic elephant tooth would, however, have been slight.

In the *true elephants* the chin has become very short, the back of the skull very high with a great amount of spongy bone, and the teeth are highly modified. They have increased greatly in size over those of the mastodonts, and have developed much higher and more numerous ridges, the valleys being filled with cement in a manner reminiscent of the molar teeth of the later horses. The shortened jaw has room for only one grinding tooth at a time. There are six grinding teeth in each row—three premolars and three molars—and as the tooth in use is worn out it is replaced from behind by the irruption of the next of the series. Each tooth comes in obliquely, so that its grinding surface lies at an angle to the true crown, and the front part of the tooth is worn thin before the back part comes into use. The great length of life of the elephants is correlated with this provision for conserving their teeth.

Among the true elephants are the African and Indian species of today, of which the former is much the more primitive, and a number of extinct Pleistocene forms. All our North American species were members of the same subfamily as the mammoth, no relatives of the Indian and African elephants having reached this continent. Of these Pleistocene species the mammoth, which occurred in both the Old and the New Worlds, is the best known. Our knowledge of it comes in part from life-like drawings and carvings made by early man, in part from the study of frozen carcasses found in Siberia and Alaska, as well as of abundant skeletal remains. Unlike any of the other known proboscidians, it was covered with an outer coat of long coarse hair over an inner layer of fine woolly hair and was further protected from cold by a layer of fat as much as 3 inches thick in places. Its tusks sometimes attained the enormous length of 16 feet. Characteristically northern, at the maximum of the glacial stages it ranged south into Florida. Other American elephants include the Columbian, Jeffersonian, and Washingtonian mammoths, of the southeastern states, Mississippi Valley, and Pacific Coast, respectively, and the immense imperial mammoth. The latter, which ranged from Florida to the Pacific Coast and south into Mexico, reached a height of 14 feet at the shoulder, while the largest modern Indian elephants stand 10 feet 6 inches high and the African elephant 11 feet 4 inches. In Europe there occurred during the Pleistocene the straight-tusked elephant and the southern elephant as well as the mammoth; all three were contemporaries of early man.

CHAPTER XXXI

Man's Relatives: The Primates

The order of mammals that interests us most is the Primates, for it is to this order that we ourselves belong, together with those animals most similar to us. In this group, just where we should like to have it most complete, the fossil record is unfortunately very fragmentary, and if we had to depend on it alone for deciphering the history of the Primates, little of their story would be known. Fortunately, many of the more primitive groups of this order are represented by modern descendants to which we can turn for interpretation of the paleontological data bearing on man's relationships, and we shall begin by considering these.

THE LIVING PRIMATES

The existing primates belong to three groups, the lemurs, the tarsioids, and the anthropoids. The members of all three share the following features: hands and feet prehensile, or evidently derived from the prehensile type; a clavicle or collarbone present; some or all of the fingers and toes with flattened nails instead of claws; two anteriorly situated breasts as a rule; and a brain that may attain relatively great size and intricacy of pattern.

The Lemurs (***Lemuroidea***). Lemurs are small, four-footed, squirrel-like arboreal primates, most numerous in Madagascar but also found in the tropical forests of Africa and the Oriental region. They are very primitive in structure, only a little more advanced than the tree shrews (insectivores) from which they were probably derived. The muzzle is long, the tail well developed; the eyes are directed outward and are surrounded by a bony ring that does not form a complete socket; some of the toes usually bear claws instead of nails; and connections with the uterine wall occur in groups all over the surface of the placenta and are pulled free at birth. Fossils of this group have been found back as far as the Paleocene in Europe and North America.

The Tarsioids (***Tarsioidea***). Members of this group also are known from the Paleocene rocks but are represented today by a single survivor, Tarsius, which occurs in the East Indies. This is a creature about the size of a rat, completely arboreal and nocturnal. Features that distinguish it from the lemurs are the immense eyes, which are directed forward and are enclosed in a nearly complete bony socket, as in the higher primates; a larger development of the posterior lobes of the cerebrum, so that these overlap the cerebellum more than in the lemurs; a skull more nearly balanced on the vertebral column; and a more disk-shaped placenta, which is freed at the time of birth by shedding of part of the uterine wall.

In all these characters, Tarsius shows an approach to the anthropoids, but in some other respects, it is even more primitive than the lemurs. It is highly specialized in the possession of jumping hind legs, toes ending in flattened disks, and overdeveloped eyes. There is reason to believe that the higher anthropoids have descended from ancestral tarsioids rather than from lemurs.

The Anthropoids (***Anthropoidea***). These, forming the third division of the primates, are characterized by having a much larger and more complicated brain; tear ducts opening within the complete bony eye sockets instead of on the face; eyes directed forward, having true stereoscopic vision, and a "yellow spot" on the retina, giving greater acuity of vision.

The first of the two subdivisions of the group includes the *New World monkeys* (Platyrrhini = "flat" + "nose"). They have the nostrils directed forward and separated by a low, wide septum; each jaw has three premolar or bicuspid teeth on each side; there are no callous areas on the buttocks. There are two families—the Callitrichidae, or marmosets, (squirrellike forms with the big toes nailed and not opposable, the remaining toes with claws, the body covered with short fur, and the tail bushy and not prehensile); and the Cebidae, or South American monkeys. The latter are of several types—capuchins (hand-organ monkeys), howlers, squirrel monkeys, woolly monkeys, etc. In all these, the toes have nails instead of claws, and the tail is generally more or less prehensile.

The second subdivision of the anthropoids is called the Catarrhini ("narrow" + "nose"), because the nostrils are usually directed downward, and the nasal septum is narrower. This group includes three families—the Old World monkeys (Cercopithecidae), the "manlike apes" (Simiidae), and extinct and recent men (Hominidae). All the members of these three families have the same tooth formula as man—two incisors, one canine, two premolars, and three molars on each side of each jaw. The toes and fingers all have flattened nails; and the tail (which may be long, short, or rudimentary) is never prehensile.

The Old World monkeys (Cercopithecidae) comprise many genera and species. All have callous areas on the buttocks, devoid of hair, which are called *ischial callosities;* these are often brilliantly colored, especially in the males. In one group, the thumb is vestigial, the hind legs are longer than the front ones, there are no cheek pouches for holding food, and the stomach is large and complicated, as in animals that chew the cud; these are herbivorous

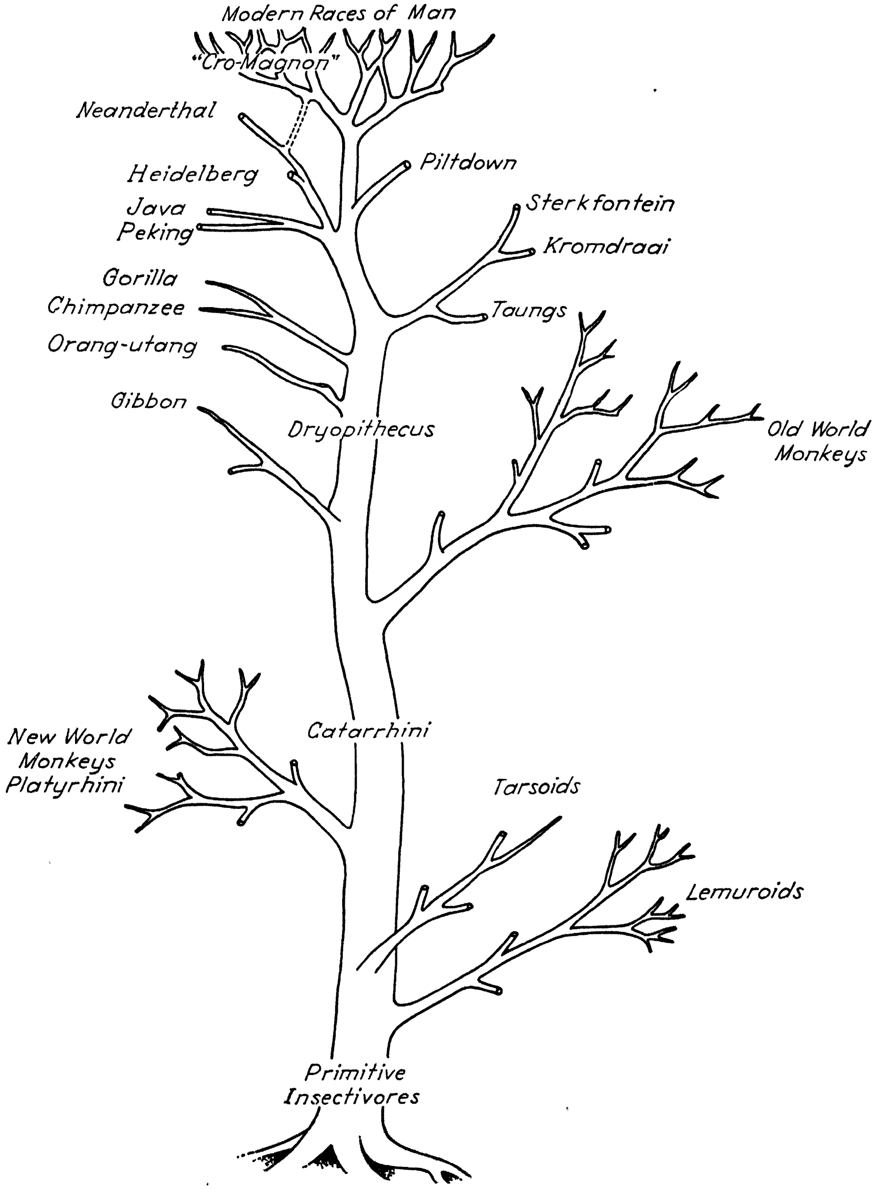
Modern Races of Man
"Cro-Magnon"
Neanderthal
Heidelberg
Piltdown
Java
Peking
Sterkfontein
Kromdraai
Gorilla
Chimpanzee
Taungs
Orang-utang
Gibbon
Dryopithecus
Old World
Monkeys
New World
Monkeys
Platyrhini
Catarrhini
Tarsoids
Lemuroids
Primitive
Insectivores

FIG. 135. *Diagram of primate relationships.*

The other chief group includes the baboons, macaques, drills, mandrills, guenons, and mangabeys. In these, the thumb is well developed, the hind legs are not longer than the front ones, cheek pouches are present, and the stomach is simple. Some of the members of this second group are arboreal. Others, like the mandrills, drills, and baboons of Arabia and Africa, have taken to the ground and have undergone considerable modifications; the muzzle is elongated like that of a dog, the canine teeth are tusklike, and the animals walk on all fours upon the palms of the hands and the soles of the feet, though the thumbs and great toes remain opposable. Baboons are quite intelligent, gregarious and act in concert for attack and defense. In many anatomical details, the Cercopithecidae approach man more closely than any of the families of primates hitherto considered; but quite evidently they are somewhat distant allies.

The Manlike Apes. Of all animals, the "anthropoid" apes of the family Simiidae come closest to man in structure, physiology, and behavior. They are distinguished from the Old World monkeys in lacking external tails, cheek pouches, and (except in the gibbons) ischial callosities; the arms are longer than the legs; the chest is comparatively wide and shallow, with a broad sternum; the pelvis is laterally expanded; the thumb is opposable in both hands and feet; and a vermiform appendix is present. They have brains larger than those of the lower primates, more like that of man in pattern and organization. The habitual posture is semierect, and the viscera are suspended in the abdominal cavity more as in man than as in the lower primates.

The Gibbon. This is the smallest of the manlike apes (in contrast the other three are often called the "great apes"). The arms are extraordinarily long, the finger tips touching the ground when the animal stands erect; the buttocks have small naked callosities, the pelvis is but little broadened, the spine has no lumbar curve, and the canine teeth are greatly elongated. The body is very slender and light, covered with fur rather than with coarse hair, as in the great apes. The hand is long and narrow; the thumb short, opposable, with a flat nail, but the fingernails are very narrow. The skull is low, with prominent brow ridges, flat nose, and protruding jaws.

The gibbons have developed the mode of progression called *brachiating* (arming) to its highest point. They swing themselves through the air from branch to branch, easily clearing distances of 20 feet and on occasion as much as 40 feet. The feet are doubled up close to the body, and the arms are used alternately, taking off with the right, catching momentarily with the left to gain impetus for a new leap, and so on indefinitely. Such locomotion calls for great agility, exact coordination, precise judgments of distance and strength of branches, good eyesight, and general alertness. There are several species of gibbons, all belonging to the genus Hylobates.

The Orangutan. This great ape is confined to the islands of Borneo and Sumatra. It is a bulky and very powerful animal, but, because of the shortness of its legs, it is only about 4 feet tall. The arms are very long, with a span of 7 to 7½ feet; the abdomen is prominent, the chest barrellike, and the buttocks small. Full-grown males weigh about 160 pounds. The hands and feet are very long and narrow, with small opposable thumbs and great toes; all the fingers and toes have flat nails. The head is large, but with relatively small brain; the brow ridges are small, the muzzle large and protrusive. The canine teeth are large, tusk-like, and interlocking. Adult males have bony crests on the top of the skull, to which are attached tremendous jaw and neck muscles. The body is sparsely covered with long, reddish brown hair. Orangs have 12 pairs of ribs, as in man; the other three manlike apes have 13 pairs. The wrist contains an extra bone not found in the other apes and man.

These apes are almost exclusively arboreal; they build nests on which to sleep and on rainy nights are said to cover themselves with leaves. Because of their weight, they climb deliberately and test the strength of branches before trusting themselves to them. On the ground, they generally go on all fours, though they can walk upright with difficulty. Orangs feed upon fruit and foliage. One young is produced at a birth, and the life span is about forty-five years, the animal becoming adult when about ten or twelve years old. There is apparently only one species, *Simia satyrus*.

The Chimpanzee. There are at least two species of great apes that go under this name, the common chimpanzee and the bald-headed chimpanzee, both belonging to the genus Pan. They inhabit a large part of the tropical forests of Africa. Chimpanzees are large, powerful, and heavily built. The male may stand 5 feet high and weigh up to 175 pounds; tests show that a full-grown male is about four and one-half times as strong as a well-developed human athlete. The legs are longer and the arms shorter than those of the orang; the hands and feet are long and narrow, with opposable but small thumbs and great toes; all the fingers and toes have flat nails. The trunk is thick, the abdomen rounded; the body is covered with black hair except on the face, hands, and feet, and in the case of the bald-headed chimpanzee, the top and sides of the head. The skull is large but low-vaulted, with brow ridges more prominent than in the orang but less so than in the gorilla. The muzzle is prominent, the canine teeth large and projecting but smaller than in orang and gorilla.

Chimpanzees are expert climbers and brachiators but spend much time on the ground, where they run on all fours or occasionally walk erect for short distances. They eat fruit and leaves and occasionally take animal food. One young is generally produced at a birth. Maturity is reached at eight to twelve years, and the span of life is probably comparable with that of man.

The Gorilla. This ape inhabits a more restricted area of tropical Africa than does the chimpanzee. There seem to be two varieties or species of the genus Gorilla, the lowland form of the west coast and the mountain gorilla, which lives at an altitude of about 10,000 feet in east-central Africa. The gorilla is the largest and strongest of the primates. Adult males attain a stature of more than 6 feet and generally weigh from 200 to 400 pounds. The largest male on record is said to have been 8 feet 8 inches tall, with an arm reach of more than 9 feet and a weight of about 500 pounds. Weight for weight, the gorilla is several times as strong as a man.

The legs are relatively short and weak; the arm is more human in proportions than in other apes; the hand is broader and shorter, more like that of man, with the thumb larger and more fully opposable than in the other large anthropoids. The foot also shows an approximation to that of man; although the great toe is still opposable, the toes are shorter, the heel better developed, and the weight is placed upon the sole to a greater extent than in the other apes. The body is covered with long black hair except on the face, hands, and feet; the hair is thin on the chest.

The head is massive, especially in males; the brain case is small and in adult males has large dorsal crests, to which are attached the powerful jaw and neck muscles; the forehead is low, with heavy supraorbital bony ridges; the jaws are protuberant and immensely strong. The nose is long, low, and narrow at the root and has a suggestion of a bridge, thus approaching that of man more closely than do the noses of other apes. The teeth are enormous, especially the canines.

Gorillas live mostly upon the ground, though they frequently climb trees. On the ground, they normally go on all fours, but when attacked or attacking, they walk erect. Although the mountain gorilla is said to be timid and peaceable, old males of the lowland gorilla are sometimes belligerent and aggressive. These apes seem to be ground-feeding herbivores that eat enormous quantities of plants and their fruits.

The Family Hominidae. Modern Man. Although man is unquestionably one of the giant primates and is more closely allied to the members of the family Simiidae than to any other animals, he differs from all the great apes sufficiently to be placed in a separate family.

The chief anatomical features distinguishing man from the apes and lower primates are: (1) the posture is fully erect; (2) the legs are much longer than the arms; (3) the human nose has a prominent bridge and a well-developed, elongated, peculiar tip; (4) there is a median furrow in the upper lip of man, and the lips are rolled outward so that the mucous membrane is visible as a continuous red line; (5) man has a chin; (6) the spine has a forward convexity in the small of the back called the *lumbar curve;* (7) the great toe is not opposable to the other toes and is in line with them, instead of being set off on the side like a thumb; (8) the foot is arched both transversely and from front to rear; (9) the body is relatively hairless and is completely devoid of long tactile hairs; (10) the brain is from 2.5 to 3 times as large as that of the gorilla, which has the largest brain of any ape; (11) the canine teeth project slightly, if at all, beyond the level of the other teeth, and the upper and lower canines do not interlock so as to make gaps—in the upper tooth arch for reception of the lower canines and in the lower tooth arch for reception of the upper canines.

Some of these characters are quantitative rather than qualitative differences, as, for example, the amount of hair on the body and the pronounced lumbar convexity of the spine, which is foreshadowed in the great apes. The depressed tip of the nose peculiar to man is somewhat like that of the proboscis monkey, and the prominent bridge is weakly indicated in the gorilla. The essentially supporting type of foot is closely approached by that of the gorilla, though the size, position, and nonopposability of the great toe are specifically human characters. The enormous size of the brain is the preeminently human feature, though its form and pattern are essentially those of the higher Primates. The supporting foot and elongated legs are evidently adaptations to life upon the ground. The general build of the foot is that of a primate, and that of an originally prehensile organ which has changed in function.

Degrees of Relationship among the Higher Primates. Man is most like the chimpanzee in weight and limb proportions, although the length of the legs is most nearly paralleled in the gibbon. The gorilla has hands, feet, and pelvis most like those of man and in size of brain is closest to the human type. The skull of the chimpanzee is more like that of man than the skull of any other ape, and the pigmentation of the skin shows a range comparable to that found in man. The orangutan is most like man in having the same number of ribs and relatively high forehead. The gibbon resembles man in length of legs and flatness of chest. In posture and gait upon the ground, the gibbon most nearly resembles man; the gorilla comes next, then the chimpanzee. All other anthropoids are much further removed in degree of resemblance.

If we turn to the most striking differences, we see that the gorilla departs farthest from man in the enormous development of its jaws, the orang in the shortness and degenerate character of the legs and in the adaptation of the feet for suspension; the gibbon differs most in excessive arm length, general size, spine curvature, shape of pelvis, hands, and feet, character of hairy covering, and length of canine teeth.

Thomas Huxley, in his epochal essay "On the Relations of Man to the Lower Animals," demonstrated that "whatever system of organs be studied, the comparison of their modifications in the ape series leads to one and the same result—that the structural differences which separate man from the gorilla and the chimpanzee are not so great as those which separate the gorilla from the lower apes." He therefore concluded that man must be classified as one of the primates, which, of course, implies descent from primate ancestors and relationship in some degree to other existing species of primates.

Schultz studied the *embryology* of 21 features of difference between man and the great apes and found that during fetal life, "all differences between human races and between man and apes or monkeys increase during some periods of growth and remain the same during other periods, but they never become less with advancing development. This constitutes strong support for . . . monophyletic origin of the human races and one common ancestry for all the primates."

These results of anatomical study are supported by many other lines of independent evidence. When anti-human blood serum is used for *precipitin tests* of the serum from other animals, the reaction obtained with that of the great apes is almost as pronounced as that obtained with the serum of man; the reaction to the blood of Old World monkeys is weaker, that to the blood of the New World monkeys is weaker still. The blood of lemurs and Tarsius gives little or no reaction, and that of lower mammals practically none. These blood tests indicate that man is very closely related to the Simiidae, more distantly to the Cercopithecidae, Cebidae, and Callitrichidae, and very remotely to the Lemuroidea and Tarsioidea. The diameters of the *red blood corpuscles* increase from the lemurs to man, and those of the great apes are closest to those of man in size.

A number of *diseases* of man are also transmissible to or normally occur among the higher Primates and are unknown in other mammals; among these are syphilis and malaria. In the case of the former, the virulence of the disease increases with nearness of the relationship of the animals to man and is greatest in the chimpanzee. The *protozoan parasites* of the higher anthropoids show a striking similarity to those of man and are in many instances apparently identical, as shown by Hegner in 1928. This author concludes that they furnish important evidence in support of the view that anthropoids and man are of common descent.

THE EVOLUTION OF THE PRIMATES

In early Cretaceous times, the lands were covered with forests, but there was little development of a ground vegetation. This may account for the fact that the early placental mammals, like the early marsupials, appear to have been arboreal. During the late Cretaceous, an upland flora came into existence that tremendously increased the possibilities for terrestrial mammalian life, and at this time, many mammalian stocks foresook the trees and took to the ground. These developed, on the one hand, into carnivores and some additional groups in which the digits are provided with claws and on the other, into the hoofed and herbivorous groups of ungulates. The insectivore ancestors of the primates were among those stocks which remained in the trees; they were probably very similar to the modern forms called *tree shrews.*

The further evolution of the primates has been a history of increasingly perfect adaptation to life in the trees, until the direction of modification was partly reversed among the larger and heavier apes and more completely in man. Even in man, however, the arboreal life of his ancestors has left its mark deeply imbedded in his structure and is probably in large measure responsible for the attainment of his present estate. Some of the more important primate characteristics, related to this arboreal habit, are discussed below.

For locomotion in trees, flexibility of the limbs is essential; this is particularly true of the forelimb, which reaches for new holds, grasps, and clings, while the hind limbs support the weight of the body. The result is the differentiation of a more *mobile arm* and more *prehensile hand,* and of a more *stable hind leg* and generally *less supple foot.* There is no restriction of limb movement to one plane, and there is no solidification of the pentadactyl foot into a stable supporting structure, as in terrestrial quadrupeds. The flat, protective nails of the digits are characteristic primate features, replacing the sharp claws of the ancestral stocks. In many of the higher Primates, *brachiation* has largely superseded climbing and jumping, and this has been accomplished by strengthening of the arms and hands at the expense of the legs and feet. On the ground, four-footed locomotion is the rule among the Primates, only the higher anthropoids showing a tendency to walk on the hind legs; but both tarsioids and anthropoids rest in a squatting position and with the hands, thus freed from a supporting function, pick up food and other objects. The primitive long tail is retained in the lower primates but tends to be shortened and reduced to a mere rudiment in the higher anthropoids; no external signs of it are present in the great apes and man.

Arboreal life has had a profound effect upon the sense organs. Smell becomes of relative unimportance, whereas to a ground dweller, it is the most important sense except perhaps touch. Good eyesight and well-developed touch and muscle senses are of greatest value. Among the Primates, there has been a progressive change in visual apparatus, carrying the eyes from the sides of the head to the front, so that the visual fields overlap or coincide, making possible stereoscopic vision. Monkeys, great apes, and man are unique in having a "yellow spot" (*macula lutea*) in the center of the retina, in which a maximum of detail can be clearly seen. With improvement in vision goes a deterioration of the sense of smell, which is probably more rudimentary in man and the apes than in any terrestrial placental.

The brain has been greatly enlarged and specialized in relation to the requirements of arboreal existence. Brachiation probably requires the most perfect coordination of muscular movement of any type of mammalian locomotion except perhaps flight; the motor and coordination centers are correspondingly developed. Keen eyesight and the ability to grasp and handle objects greatly increase sensory perceptions, and this has been accompanied by overgrowth of the cerebral hemispheres in which the sensory areas are located. A constantly increasing brain size has been a characteristic of primate evolution.

Changes in brain and sense organs have been accompanied by *changes in skull form and in dentition.* The muzzle has shortened; the brain case has increased in size. The shortening jaw has lost a part of the original complement of 44 teeth, the number being reduced to 32 in Old World monkeys, the great apes, and man. The teeth are little specialized and resemble those of the omnivorous pig and of the early ungulates, the molars being low-crowned and having rounded cusps; man differs from the other primates in the more reduced canine teeth.

In primitive mammals, the eye socket is not separated from the temple opening. In many of the more advanced mammals (for example, the horse), a bony bar bridges the space and separates the two openings; such a bar is found in all Primates, even the lowest. But in addition, the tarsioids and anthropoids have developed beneath this bridge a sheet of bone that encloses the eye socket—a structure found in no other animals. Presumably it gives better muscle attachment and support for the eyes in their rotated position and prevents disturbances of vision caused by movements of the jaw muscles.[1]

Fossil Primates. Remains of this group are rarely found, except those of late-stage man, who practiced burial. Primates are for the most part arboreal and tropical. Forest dwellers are less likely to be buried in sediments than inhabitants of gullied plains and flood-swept river valleys, and humid tropical regions are favorable to rapid decay and destruction of dead bodies.

The oldest known fossils are *lemuroids* and *tarsioids*, from the Paleocene and Eocene of North America and Europe. It seems quite certain that the anthropoids of the New and Old Worlds developed from different members of the tarsioid stock. The earliest ancestral catarrhine monkey occurs in the Lower Oligocene of Egypt. This creature, *Parapithecus*, was smaller than any existing Old World monkey; it was very primitive and may well represent the stock from which the modern Cercopithecidae, Simiidae, and Hominidae have evolved. It already had the reduced number of teeth characteristic of the catarrhines, the dental formula being the same as that of man. From this stock, the tailed monkeys of the Old World (Cercopithecidae) diverged during the Oligocene and Miocene; they have specialized along lines divergent from those which led to the human type and do not represent any stage in human evolution.

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[1] Hooton gives a very good and full account of the changes that have occurred in the evolution of the Primates in his book *Up from the Ape.*

The stock that led to the great apes, on the one hand, and to man, on the other, apparently originated at almost the same time as the cercopithecids, for the oldest apelike fossil, *Propliopithecus*, was also found in the Lower Oligocene rocks of Egypt. This was a small, gibbon-like animal, probably standing about 20 inches high. It was much less highly specialized than the modern gibbon and probably lies close to the line from which man and the manlike apes have descended. Pliopithecus, from the lower Pliocene of Germany, is almost a full-fledged gibbon and, as such, is off the main track of human ancestry.

During the Miocene, the *giant primates* appeared, evidently developed from some of the smaller and more primitive Oligocene forms. Remains of giant anthropoids of this age have been found in India, in Egypt, and in several European localities. The Middle Miocene types had advanced far in structure toward the orangs, chimpanzees, and gorillas, and probably toward man. Paleosimia, from India, is almost certainly an ancestor of the orang. The orang line would appear to have split off from the primitive great ape-human stock in northern India at a time prior to the differentiation of the latter into the gorilla and chimpanzee lines, on the one hand, and the fossil African manlike primates and man himself, on the other.

The common ancestor of all the latter types may perhaps be represented by *Dryopithecus*, a Miocene genus, of which at least six species are known. Some of these appear to lead in the direction of the gorilla or chimpanzee, others to be intermediate in characteristics, and all of them are close to the type from which the Hominidae must have come. The common ancestor of man and the great apes would thus seem to have lived in the early Miocene or perhaps as long ago as the late Oligocene and to have been either Dryopithecus itself or its immediate precursor.

There is little direct fossil evidence of the course of primate evolution during the Pliocene; but since 1925, there have been found in South Africa three remarkable fossil primates of Pleistocene age, which may be regarded as somewhat modified holdovers from the Pliocene stock that gave rise to man. These were large-brained apes that in many respects, especially in the structure of the skull and teeth, resemble man more closely than the chimpanzee and gorilla do. The oldest and most apelike of these is the early Pleistocene Taungs skull (*Australopithecus africanus*), discovered in 1925; distinctly closer to the human type is the late Pleistocene Sterkfontein skull (*Plesianthropus transvaalensis*), found in 1936, of which additional material was obtained in 1938; and most interesting of all is the recently discovered Kromdraai skull (*Paranthropus robustus*), of middle Pleistocene age, found in 1938 not far from Sterkfontein.

According to Dr. Robert Broom, the discoverer of the two last-mentioned fossils, Paranthropus may truly be described as the long-sought "missing link" between man and ape, so far as structure is concerned, though being a contemporary of extinct human species, he must be only a "cousin" and not an ancestor of man. This man-like fossil ape lived about 300,000 years ago and was probably much like the Pliocene forms from which man developed. It was larger than the male chimpanzee and smaller than the female gorilla but resembled neither of these apes. The brain case was small and the muzzle protruding, as in the other apes; but the cheekbone, jaw hinge, and dentition were almost as in man. The resemblance is particularly striking in the case of the teeth. The tooth row forms a broader arch than in modern apes; the canine teeth are no larger than the others and are very human in shape; and the molars show an approach to those of man. Furthermore, the foramen magnum is farther under the skull than in the gorilla and chimpanzee and indicates that the animal walked more nearly erect than the latter.

The history of the development of the highest of the Primates, man himself, as recorded by fossil remains and the sequence of human cultures, is the subject of the succeeding chapter.

CHAPTER XXXII

The Paleontological Record of Human Evolution

At a time when remains of apelike men were still unknown, Darwin postulated that such creatures must have existed. It is interesting that before his death in 1882, fossils of men with simian characteristics had been found. Since 1895, scarcely a year has passed without the discovery of at least one new specimen of fossil man or of fossil apes with manlike characters. In recent years, concerted efforts on the part of great scientific organizations, universities, governments, and individual scientists not only have testified to the widespread interest in human origins but have resulted in greatly increasing our knowledge of man's ancestry. Hundreds of thousands of dollars have been spent in the search for more evidence, and the results have amply repaid the cost. In a sense, the search for the famous (or infamous) "missing link" may be said to be practically finished; not one, but many links in the chain of relationship between man and the other anthropoids have been found. Although the fragmentary nature of many of the older remains, the continual discovery of new evidence, and the differences in the interpretation placed upon the data by various students have led to disagreement over the details of human evolution, there is ever-increasing unanimity concerning its broad outlines. The new discoveries of recent years have cleared up many of the earlier points of issue, even while they have raised new problems.

The story of man's development has been pieced together from many kinds of evidence, some indirect, like that from comparative anatomy, embryology, and physiology, and some direct—the evidence of ancient human bones and the remains of human cultures. The data from human fossils and those from fossil cultures form two lines of parallel evidence, sometimes merging, as when fossil men are found together with the implements and other artifacts they made, and sometimes running alone, as when fossils or cultures are found unassociated with each other. We shall trace the development of human cultures a little later, after having considered the more important of the fossil men.

The Pleistocene Glacial and Interglacial Stages. The entire known history of man is comprised within the Pleistocene and can be understood only in relation to the changing conditions and great climatic disturbances that characterized this epoch. As a whole, the Pleistocene is often spoken of as "the glacial period," but it was not one long ice age or, indeed, the only time in earth history when glacial climates existed. We have already seen that glaciation occurred during the Permian, and there are records of extensive glacial action as far back as the Proterozoic. The Pleistocene ice sheets were here so recently, however, that their work is evident over great parts of the Northern Hemisphere; and the ice sheets of Greenland and Antarctica are present to remind us that the ice ages are not long past or that perhaps the glacial period is even yet not finished.

The history of the Pleistocene climates is that of a succession of cold, glacial times alternating with longer warm intervals. During the cold stages, vast ice sheets spread from the north and from the higher mountains over North America and Europe, carrying the animals and plants of the arctic and subarctic zones far south of their present limits and crowding the fauna and flora of temperate climates farther toward the south. Each of these glacial stages lasted a very long time—long enough for the ice sheets to reshape the land over which they crept and to deposit great quantities of soil and rock along their southern edges. But eventually, after thousands or tens of thousands of years, the climate would again slowly become warmer; the ice sheets would melt away from the south northward and eventually disappear from most or all of the northern continents. As this change continued, the temperate and warm-climate faunas and floras would gradually spread northward again in the wake of the retreating glaciers. These warm intervals are known as the *interglacial stages.* They were at least as long as the glacial times, and one of them, at any rate, was very much longer. There is evidence that their climates were at times even warmer than those of today, since warm-temperature animals like the hippopotamus and lion spread to England, and leaves of pawpaw and other deciduous trees occur in interglacial deposits near Ottawa, Canada, in a region now dominated by northern coniferous forests.

In both North America and Europe, there seem to have been four principal times of cold climates and glacial advance, separated by warm intervals of varying duration. Different names have been given to these stages in North America and in Europe; but since the record of human evolution is largely found in the Old World, the European names are used in this account. The glacial stages are (1) Günz, (2) Mindel, (3) Riss, and (4) Würm. The interglacial stages are the first, or Günz-Mindel, the second, or Mindel-Riss, the third, or Riss-Würm, and perhaps postglacial, or Recent time. The second interglacial stage, the Mindel-Riss, was longer than the others and may have endured more than 300,000 years. Postglacial time is generally estimated at about 25,000 years. Knowledge of the names and sequence of the Pleistocene stages is necessary if one is to follow the history of human development; and frequent reference should be made to the accompanying chart (p. 432, fig. 138) showing the approximate time relations of the fossils and cultures.

FOSSIL MEN

Prior to the time, late in human history, when man began to bury his dead, preservation of human skeletal material was a rare accident. Nearly all the older fossils of man have been found in stream or cave deposits. The bones are usually scattered; complete skulls are rare. The earlier students of ancient man had to work with fragmental and imperfect material, and it is a monument to their skill and insight that in so many respects the more abundant materials found in recent years have borne out their conclusions. The criteria that, in general, have been used in distinguishing between human and anthropoid ape fossils are of two sorts: (1) definite association with artifacts and traces of the use of fire and (2) anatomical features, including large cranial capacity considerably exceeding that of any great ape and approaching that of modern man, the less reliable features of the jaws and teeth, the characteristically human type of pelvis, and the elongated leg bones and flattened, walking foot peculiar to man.

Opinions naturally vary as to the proper classification of the fossil types of man and their relations to *Homo sapiens*. According to one interpretation, advanced by Sir Arthur Keith and accepted with some reservations by Prof. E. A. Hooton, of Harvard University, three main stocks may be recognized within the human family. The first, and that best represented among the older fossils, includes Java man and Peking man and their relatives or descendants, Heidelberg man and Neanderthal man. The second stock, of problematical relationship to the other two, is represented by Piltdown man. The third, very poorly known as to its antecendents, includes the Upper Paleolithic and later men of Europe and all the races of modern man. Not all students agree to this interpretation, which is, indeed, probably much oversimplified. A considerable group of anthropologists, of whom the well-known American authority Aleš Hrdlička is one, hold that modern man developed directly from Neanderthal ancestors.

***Java Man and Peking Man* (*Pithecanthropus and Sinanthropus*).** The two most primitive types of man have both been found in Asia. In 1891, the French physician Dubois discovered a skull vault, part of a lower jaw, three teeth, and a left femur near Trinil, Java, in river gravels that have since been definitely established as of Middle Pleistocene age (corresponding to the second interglacial stage in Europe). These remains, which he named *Pithecanthropus erectus* (the erect ape man) are without doubt the most famous of all fossils, for they seemed to bridge the gap between man and the higher apes in a most remarkable fashion. They have been intensively studied, and thousands of pages have been written about them. Some students thought that Pithecanthropus was a very primitive and apelike man, others that he was a very advanced and manlike ape, and prolonged controversies raged over his status. Of course, such disagreement between scholars served only to emphasize the intermediate position of Pithecanthropus. Much later, in 1932 and 1935, Dubois published descriptions of five additional femora of Java man that had been in his possession for some 40 years. Since 1936, our knowledge of this ancient type has been greatly augmented by the discoveries of G. H. R. von Koenigswald, working under the auspices of the Carnegie Institution of Washington. He has obtained parts of three adult craniums and additional jaw fragments from Middle Pleistocene strata at Sangiran, Java; and at Modjokerto, Java, the brain case of a young Pithecanthropus child was found in the Djetis formation, a lower Pleistocene deposit that underlies the Middle Pleistocene Trinil beds.

Meanwhile, in 1927, Dr. Davidson Black of Peiping Union Medical College, had recognized a very primitive human tooth among some fossils found in cave deposits at Choukoutien, 37 miles from Peiping (Peking), China. On the morphological characters of this tooth, he established a new genus and species of fossil man, *Sinanthropus pekinensis.* With the aid of W. C. Pei, intensive work was begun on the cave deposits, with the result that additional teeth, portions of jaws, and one nearly complete brain case had been found up to 1929. Since the death of Dr. Black, the work has been continued by Franz Weidenreich and Dr. Pei; in all, some 40 skulls, mostly fragmental, and some other bones have been found. A controversy developed as to the relative age and primitiveness of Peking man and Java man, but a recent cooperative study of all the fossil material by von Koenigswald and Weidenreich has brought them into essential agreement. Pithecanthropus and Sinanthropus prove to be so nearly alike in all important respects that they must have been very closely related; the differences are stated to be no greater than those between many modern races. The two forms existed contemporaneously and over a very long period. The bulk of the material of both is from the Middle Pleistocene, approximately half a million years old; and the juvenile Modjokerto Pithecanthropus skull and a single implement characteristic of Sinanthropus from the Lower Pleistocene at Choukoutien carry the known existence of both forms back to a far earlier period, perhaps three-quarters of a million years ago.

The skull and brain of Peking man, although definitely human in their essential features, are very different from those of any member of our own species and show many apelike characteristics. The skull is long, low-vaulted, and relatively narrow, with a very low and sharply receding forehead. The bony ridges over the eyes are huge and continuous, as in the chimpanzee. The nasal opening shows that the nose was broad and flat, with a deep impression at its base. The jaw is massive and apelike and has practically no chin, so that the mouth and lips must have formed a muzzlelike projection, with the chin region curving back sharply from the base of the front teeth. The part of the jaw that rises from the back to hinge against the skull is of human shape but is almost vertical instead of sloping backward, as in most modern skulls. The teeth have the pulp cavity that contains the nerve and blood supply of the tooth greatly enlarged. In this respect, they resemble those of Heidelberg man and Neanderthal man and differ from those of apes, Pithecanthropus, and modern man.

In Sinanthropus, as in Pithecanthropus, the brain case is very apelike in appearance. It is widest low down and rather far back, just in front of the ears; the crown forms a low, flat arch from front to back, and the sides slope from the widest point directly inward toward the middle line, instead of first outward and then inward, as in modern skulls. In spite of its apelike form, the cubical capacity of the brain case much exceeds that of any ape, though it is small in comparison with that of modern man. The range in Peking man is from 850 to 1,220 cc., with the average about 1,000 cc. The larger skulls are believed to be those of males, and the sexual difference in size appears to have been unusually great in both this species and Pithecanthropus. The cranial capacity overlaps the range of modern man, in whom racial averages for males vary from 1,200 to 1,500 cc., and the individual extremes are 910 cc. (a Peruvian Indian skull) and 2,100 to 2,200 cc. (skulls of a Potomac Indian and of the Russian author Turgenev). By contrast, the cranial capacity of orangs, gorillas, and chimpanzees ranges from 290 to 610 cc. The calculated ratio of body weight to brain weight in modern man is about 50:1; in Sinanthropus and Pithecanthropus, about 90:1; and in the orangutan, about 180:1. Casts of the interior of Java and Peking craniums shows that the brain was primitive in form, with much less development of the frontal lobes than in modern man but much more than in the gorilla. From a study of brain casts of Pithecanthropus, Tilney concluded that, among other advances over the apes, this creature may have been capable of speech.

The skull of Java man is a little smaller and less capacious than that of Sinanthropus; the huge brow ridges are less demarcated from the very low and receding forehead; and the molar teeth are somewhat larger and the lower incisors and canines smaller. The upper canine teeth of both Java and Peking man are protruding and tusklike, though much less developed than in the apes; but Java man is unique among fossil men in having a gap in the upper tooth row between the canine and the lateral incisor, into which the somewhat tusklike lower canine fitted. This gap is nearly as large as that in the male gorilla and is the same size as that in the male orang. Some of the skulls, jaws, and teeth are enormously heavier and larger than others, and this is further indication of the males having been larger and stronger than the females to a degree unmatched in other human types. In Java man, the leg bones are straighter and are much more like those of modern man than in Sinanthropus; so much do they resemble our own that doubts were long expressed as to whether they really belonged with the skulls, but this now seems almost certain.

Among the many apelike features of these, the most primitive known types of men, especial attention may be called to the following: The *arch* *of the skull top* from front to back in the flattest and most gorillalike of any of the known types of man. There is an indication of a low *median crest* in the skulls of the males, absent in modern man. The *position of the foramen magnum* is just under the base of the skull, so that it is visible from the rear; this is intermediate between the condition in apes, in which the foramen is far back on the skull and points outward, and that in modern man, in whom the foramen is well under the skull and points downward. The *brain*, as shown by casts, was singularly small and flat, with the front part poorly developed, as noted above. The *shape of the tooth row* is a narrower arch than in our own species, more as in the great apes. The teeth are all large, with no indication of reduction in the wisdom tooth or last molar; they show collectively and severally many apelike features. Some of them are predominantly human in form, others more nearly anthropoid, and contrasting types of teeth are often found in the same jaw. The cusp pattern is somewhat more primitive in Sinanthropus than in Pithecanthropus, but the enlarged pulp cavities of the former are a specialization not indicated in the latter. The upper canines of males of both forms were somewhat projecting and tusklike, but the lower canines were small in Sinanthropus, presumably considerably larger in Pithecanthropus males. Weidenreich and von Koenigswald are inclined to believe that Peking man and Java man form a single group of "prehominids," related to each other in much the same way as are the races of modern man. It is uncertain which is the more primitive, though the balance of the evidence seems to favor Pithecanthropus in this respect, particularly that afforded by the size of the teeth and the gap in the upper tooth row.[1]

There is good reason to believe that Heidelberg man and his probable descendant Neanderthal man came originally from a stock similar to or identical with that represented by Java-Peking man. If, as Keith and Hooton think likely, this evolutionary line is distinct from that which led to modern man, we should have to look to the late Pliocene for their common ancestor, and in the light of recent discoveries, it is not too much to hope that fossils of such a creature may eventually be found. The possibility is not yet excluded that modern man came from Neanderthal stock, in which case we number among our more remote ancestors men of Java and Peking type. Even if our own line did have a separate development, there is good reason to believe that a certain amount of hybridization occurred between Neanderthalers and *Homo sapiens*. It is not at all improbable that from time to time during the evolution of the human stocks, groups that had become unlike through isolation and segregation again met and mingled, as man became more of a wanderer. If the germ plasm of our own species has received contributions from more than one of the early human stocks, this would help to explain our great variability and the fact that individuals occasionally appear among us with traits suggestive of one or more of the fossil types of man.

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[1] In 1944 Weidenreich announced the discovery of two new giant types of fossil man, *Meganthropus paleojavanicus* from Java (related to Pithecanthropus but about the size, stoutness and strength of a big male gorilla), and *Gigantanthropus blacki* from China (known only by three enormous fossil molar teeth, six times as large as those of modern man, and larger than those of Meganthropus).

Piltdown Man (***Eoanthropus dawsoni***). Portions of a skull and jaw of a primitive man were found by Dawson and Smith-Woodward, in 1911 and 1912, in a gravel pit at Piltdown, in the South Downs of England. For years a controversy existed as to whether the skull and jaw actually were parts of a single individual, for although the skull is much more human than those of Sinanthropus and Pithecanthropus, the jaw greatly resembles that of a chimpanzee. Discovery in 1915 of parts of a second skull and molar tooth 2 miles from the first site seems to remove doubt that the original jaw and skull belong together, since the new finds show the same characteristics.

The jaw has no chin prominence; the insertions of the tongue muscles are in a pit backed by a bony plate, as in the chimpanzee; and the lower canine tooth is a massive tusk projecting ⅔ inch beyond the level of the other teeth. These are ape-like characters; but in other features, the jaw and teeth differ from those of both ape and man or approach the latter more closely than the former. The molars are longer than broad and have five cusps, as in apes, but it is the second molar that is largest, not the first, as in man, or the third, as in apes. The wear on the molars shows that in chewing, a rotary grinding motion was used, as in man; apes chew with a vertical champing motion, the form of the jaw hinges and the interlocking canines preventing lateral movement. The jaw hinge of Eoanthropus must therefore have been of human type; and the nature of the wear on the lower canine tusk shows that it did not interlock with the missing upper canine. The latter had probably moved forward into the incisor row of teeth, leaving the lower canine opposed only by the small first premolar. The brain case is large, its capacity (1,400 cc.) being well within human range; the forehead was rather broad and high, the supraorbital ridges were weak and show human characteristics, and the skull was better poised on the neck than in Peking and Java man. The most outstanding peculiarity of the skull is the enormous thickness of the cranial walls. The face was of quite human dimensions, and the nose was apparently low and broad.

Just what relationship this creature with the advanced and altogether human brain case, forehead, and face and the massive, tusked, and ape-like jaw bears to other members of the human family is uncertain. Piltdown man could not have resembled members of the Java-Peking stock much more closely than the latter resembled an anthropoid ape. On cranial characters alone, Eoanthropus might well pass for an early member of the stock that has led to modern man; if he is on the direct line of human ancestry, then parallel reduction in the size of the jaw, changes in tooth size and pattern, and reduction in canines must be supposed to have occurred independently in the Pithecanthropus-Neanderthal line and in the Eoanthropus–*Homo sapiens* line. Furthermore, the pulp cavities in the molar teeth of Piltdown man are somewhat enlarged, though not to the extent found in Heidelberg man and Neanderthal man. Reversal of this tendency and return to the primitive small-chambered tooth found in the apes and modern man would be required for the derivation of the latter from either Eoanthropus or Neanderthal. On the whole, Keith's suggestion that Piltdown man represents a primitive offshoot from the base of the line leading to *Homo sapiens* seems the most logical interpretation of the evidence, although Hooton thinks that this type more nearly approximates the ancestral form of modern Europeans than any prototype yet discovered.

The age of Piltdown man is also somewhat doubtful. The deposits in which it was found have by some been assigned to as far back as the late Pliocene, but an early Pleistocene age has been generally accepted. However, the discovery in 1936, of a portion of a somewhat similar and perhaps even more primitive skull in river gravels of the Thames valley in England suggests a mid-Pleistocene or even later date, to judge from the artifacts that the deposits are said to contain. Perhaps Eoanthropus endured much longer than has been supposed. It seems quite likely that he was a contemporary of Sinanthropus in China, Pithecanthropus in Java, and Heidelberg man in Germany. England was still a part of the continent of Europe when Piltdown man lived there, with a great river valley where the English Channel now lies.

***Heidelberg Man* (*Homo heidelbergensis*).** At Mauer, near Heidelberg, Germany, a huge sand pit has been excavated to a depth of more than 80 feet in the stratified deposits in a valley. These were made by the gradual filling of the valley over a very long period, during which the land was slowly sinking; more recently the land has risen, and the stream is now cutting down through them and leaving them exposed on the valley sides. The pit has long been a favorite site for collecting fossils, and Schoetensack, a German geologist, visited it almost daily for 20 years in the hopes of finding traces of early man. In 1907, he was rewarded by the discovery of an almost perfect human jaw at the bottom of the pit, 82 feet below the surface, beneath 24 overlying strata.

This Mauer jaw is the largest and most powerful mandible ever attributed to a human being. It considerably exceeds in size even the massive, chimpanzeelike jaw of Eoanthropus. The body of the jaw is thick, deep, and chinless; the ascending rear part is of enormous breadth (2⅜ inches, as opposed to 1½ inches in modern man). The tongue muscles arose from a simian pit instead of from the tubercles characteristic of our own jaws; but there is no simian shelf strapping together the two sides of the jaw in front, such as regularly occurs in apes and is a feature of the Eoanthropus mandible. The jaw is short and broad, with the tooth rows diverging posteriorly, as in man, instead of being narrow, with parallel tooth rows, as in the apes.

In spite of all this, the Mauer jaw would undoubtedly have been attributed to an extinct ape had it not been for the characteristics of the *teeth*, which are unmistakably human. They are not exceptionally large; the canines are short and blunt and do not rise above the level of the other teeth, as they do in apes, Eoanthropus, and Pithecanthropus. The molars show a peculiarity in the nature of the pulp cavities; these are greatly enlarged and project well down into the jaw, the body of the tooth being correspondingly long and the roots short. Such teeth have been named *taurodont* (*taurus*, "bull" and *dens*, "tooth") in allusion to the fact that a similar condition characterizes the teeth of cud-chewing mammals, including cattle. On the other hand, in the apes, Pithecanthropus, and modern man, the pulp cavities are small and shallow and lie above the level of the edge of the jaw. Teeth of this sort are called *cynodont* (*cyno*, from the Greek *kion*, "dog"), because in this feature they resemble the teeth of carnivorous mammals. Taurodontism is strongly developed in Neanderthal man and is moderately indicated in Sinanthropus and Eoanthropus. It is regarded as a specialization away from the primitive cynodont condition.

From the nature of the Mauer jaw and some additional fragments found in the same pit in 1927, certain inferences are justifiable as to the nature of this man. His canine teeth were no longer defensive weapons; he therefore fought with his hands. The taurodont teeth suggest a diet of coarse vegetable food. He undoubtedly walked erect, though from what we know of his probable descendant, Neanderthal man, his posture was doubtless slightly stooped and bent-kneed. He may well have had some rudiments of material culture, of about the same (or a slightly higher) level as that of Pithecanthropus and Sinanthropus. It is possible that he was the maker of some of the Abbevillean hand axes, but it now seems more likely that these were the work of men more like ourselves.

In the same layer with the jaw were found bones of elephants, rhinoceroses, an extinct horse, bison, two species of bears, a lion, and other mammals. These are warm-climate animals, indicating an interglacial age for the deposit, but whether first or second interglacial is still uncertain. The probabilities favor the older period. Since Pithecanthropus and Sinanthropus existed from Lower to Middle Pleistocene times, Heidelberg man was evidently a contemporary, and even if he lived during the second interglacial, his age is not less than half a million years. If he developed from a stock represented by Java man and Peking man, as seems likely, he had progressed morphologically to a considerable degree, and his differentiation probably began early in the Pleistocene, perhaps as much as a million years ago. According to this view, the Middle Pleistocene Java and Peking men must have been the relatively unprogressive survivors of a stock widespread in the late Pliocene or

Lower Pleistocene, from which both they and Heidelberg man were descended. The taurodont specialization of the teeth of Sinanthropus, Heidelberg man, and Neanderthal man, combined with other features of resemblance, lends some support to this idea of their relationship, though it is to some degree offset by the lack of this feature in Pithecanthropus and its moderate development in Eoanthropus, the latter clearly belonging to another human stock.

***Neanderthal Man* (*Homo neanderthalensis*).** During the middle and latter parts of the Pleistocene epoch, Europe and western Asia were inhabited by a species of rather apelike men called the *Neanderthals.* Many skeletons of this species have been found in France, Belgium, Spain, Germany, Czechoslovakia, Jugoslavia, Palestine, and islands in the Mediterranean Sea. These skeletons are associated with stone implements of a type called *Mousterian,* and the Mousterian culture has a wider distribution than the known fossil remains, occurring also in the British Isles, Italy, north Africa, eastern Europe, and perhaps in China and South Africa. We cannot be sure that Mousterian implements were made exclusively by Neanderthals, but no user of these implements has been found who was not a member of that race.

The relative abundance of Neanderthal remains gives us a quite complete knowledge of the characteristics of this race. The skull was large, with a brain well within the size limits of modern man but differently shaped. In general aspect, the head was bestial, the brain case very much elongated and low, the supraorbital ridges immense, the forehead very low and retreating, and the occiput protuberant. The face was long and projecting, the orbits very large, the nose short and very broad, the muzzle prominent, and the jaw almost chinless. In profile, the brain case was about intermediate between that of the chimpanzee and that of modern man. The face was much more human than apelike but showed definite simian characteristics. The neck muscles were attached much higher on the head than in modern man; the head jutted somewhat forward from the neck and had little freedom of movement. The jaw was smaller than in Heidelberg man, showed a trace of a chin and beginnings of tubercles for the attachment of the tongue muscles. The teeth were arranged in a broad U-shaped arch, with the canines small and set in the curve and the molars taurodont. The features of the jaw have led to general agreement that Neanderthal man probably descended from Heidelberg man. The jaw hinge was somewhat apelike, and the nature of the tooth wear indicates that chewing was done mostly by a forward-and-backward movement in a manner different from that observed in modern man.

Neanderthal men ranged in height from 5 feet 1 inch to 5 feet 5 inches; women were somewhat shorter. The trunk was short and thick; the

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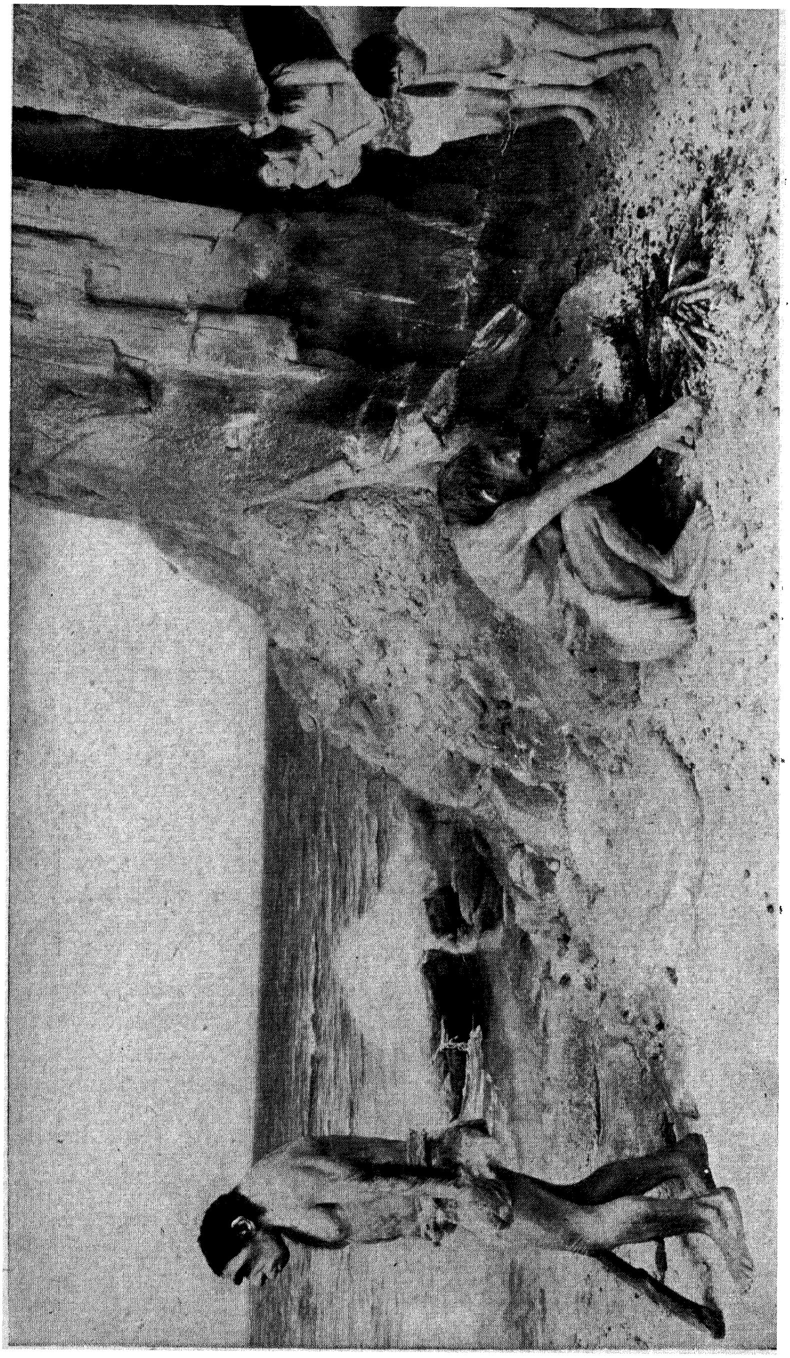

FIG. 136. *Restoration of a Neanderthal family in the shelter of Gibralter during the Fourth Glacial stage.* (*Courtesy of the Field Museum of Natural History, Chicago.*)

spine was massive, and the neck vertebrae had long spinous processes like those of the chimpanzee, very different from the bent-down and degenerate spinous processes of modern man. The shoulders were hunched forward and the head buried in the heavy neck muscles. The lumbar curve of the spine was very weakly indicated, and the pelvis was much more apelike than that of modern man. The arms were not unusually long but were extremely massive and strong, with large joints; the hand was quite human, with short digits.

The femur was strongly bowed forward, as in apes, instead of straight, as in modern man; furthermore, the knee joint indicates that Neanderthalers probably walked upright but with slightly bent knees. Modifications of the ankle bones show that these men rested in a squatting position. The foot was a supporting organ but retained some of the characters of the grasping foot that are lost in modern man; the great toe was sharply separated from the others, and the weight was supported on the outside margin of the foot, more as in the apes. Altogether, the foot was much more human than apelike.

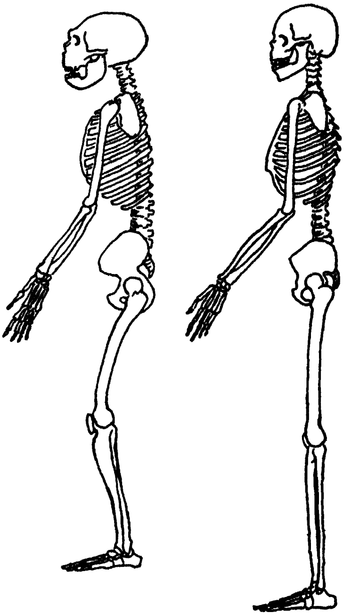

FIG. 137. *Comparison of the skeletons of Neanderthal (left) and modern man (right). (Redrawn from Lull, Organic Evolution, The Macmillan Company.)*

To judge from brain casts and from the evidences of their culture, the intelligence of Neanderthal man was certainly far superior to that of any ape and possibly but little inferior to that of some primitive men of today. This race made its homes in caves, used fire, and buried its dead; it had already developed the manufacture and use of specialized flint tools of several kinds, which served as weapons and for cutting, scraping, and other purposes. The workmanship shown by these flints indicates a considerable degree of manual precision and some ingenuity.

In Europe, men of Neanderthal type occupied the region for a very long period; but at some time after the maximum of the last glacial advance, Neanderthalers abruptly disappeared. In the caves of France, the Mousterian industry is replaced by a quite different culture, with new types of flint implements, an increasing prevalence of bone tools, and the introduction of sculpture and drawing. The men responsible for this new culture were of modern type, belonging to the same species as ourselves. Although in Europe they replaced Neanderthal man, in Palestine the two types seem to have lived side by side for some time, for remains of both have been found in cave deposits supposedly of the same period near the Sea of Galilee.

Elsewhere than in Europe and Palestine, Neanderthaloid men have been found only in Java and in Africa. Since 1936, the excavations of von Koenigswald in Java have turned up heavy, primitive Neanderthal-type skulls similar to the European ones. Their discoverer believes them to have been approximately contemporaneous with Pithecanthropus, but they represent a far more advanced type and possessed much better stone implements and weapons.

In South Africa, there was found, in 1921, a fossil man of somewhat Neanderthaloid type, which has been named *Homo rhodesiensis*, or Rhodesian man. The remains consisted of a skull without lower jaw and various other parts of two skeletons. There is, however, considerable doubt as to whether the skull and the rest of the bones belonged to the same individual. It is the skull that is the remarkable feature of this man, in any event. It possesses literally enormous brow ridges, comparable among Primates only to those of the gorilla; the forehead was extremely low and narrow and the crown little more vaulted than that of Pithecanthropus. In other respects, however, the skull is definitely human in form, and the cranial capacity is approximately 1,300 cc. The brain was apparently far inferior to that of Neanderthal man. One especially human characteristic of the rather large but definitely manlike teeth is the fact that they are badly decayed—a condition almost never found in apes and rare in most primitive men. Some authorities regard this as a variant of Neanderthal man, but it seems more likely that he represents a separate stock that originated from a common stem with Pithecanthropus during the Pliocene. The fact that the teeth show no trace of taurodontism, so marked in Neanderthal man, makes a close relationship between them improbable.

***The Coming of Modern Man* (*Homo sapiens*).** Here and there in Europe, in particular at Galley Hill in the Thames valley of England, at two places in Italy, and in various parts of France, apparently very ancient fossil men of the same species as ourselves have been found. The most famous of these is the Galley Hill man, a nearly complete skeleton discovered in 1888 in a high level terrace gravel bed of Middle or Lower Pleistocene age, which contained many implements of the hand-ax type. This man was about 5 feet 3 inches tall, stocky, muscular, with modern-type bones. The skull is long and narrow, almost identical in form with those of Aurignacian men of the Upper Paleolithic cultural stage. It has a cranial capacity of 1,500 cc., equal to that of the average modern European male. None of the features of this skull is any more apelike than those of many crude types of existing men. The very modern appearance of this fossil, together with the fact that its occurrence along with implements in undisturbed strata seemed insufficiently attested, made archeologists very loath to grant that it was as old as it seemed to be. Similar objections were raised in the case of the other finds mentioned above. Sir Arthur Keith, however, supported in recent years by Hooton, has long maintained the great antiquity of Galley Hill man in the face of these objections, and his contention has recently been verified in striking fashion.

Archeologists had been coming to suspect that the men responsible for the Lower Paleolithic hand-ax industries that preceded the Mousterian culture of the Neanderthalers were not of Neanderthal or Heidelberg stock but in all probability were the ancestors of modern man. Keith believed that Galley Hill man was one of the makers of the hand axes. This question has now been answered definitely in the affirmative by the finding, in 1933, of a skull of a man of our own species associated with Middle Acheulian hand axes. This fossil was found in the Barnfield gravel pit at Swanscombe, England, under circumstances that all agree are conclusive. The age of the stratum is Middle Pleistocene, probably second interglacial stage; the skull rested in undisturbed deposits within a few feet of the implements. This man appears to have been not unlike the Galley Hill man—longheaded, apparently representative of the basic European stock that replaced the Neanderthals sometime during the fourth glacial stage. He is *far older than the oldest known Neanderthal* and in age approximates Pithecanthropus, Sinanthropus, Eoanthropus, and Heidelberg man. If *Homo sapiens* is related to Neanderthal man, it would seem, therefore, that it must be by descent from common ancestors and not by direct descent. This discovery gives support to Keith's idea that the human stock split, late in the Pliocene, into two or three main lines of development, the Neanderthaloids (including Pithecanthropus, Sinanthropus Heidelberg man, and Neanderthal man) being one, our own line a second, and Piltdown man (if not directly in the ancestry of modern man) a third.

For a long time after the appearance of these first representatives of *Homo sapiens*, the European stage was held by the Neanderthalers, but during the fourth glacial stage, these disappeared with seeming abruptness, being supplanted by men of modern type. However, the two species may have coexisted in places for some time, as has already been mentioned. In two caves near Mount Carmel, in Palestine, numerous skeletons and associated cultures have been found by McCown. These show a peculiar comingling of Neanderthal and modern man; the skeletons vary from wholly Neanderthaloid to virtually modern types, with every combination of characters represented. It is very striking that this mixed population also shows a mixed culture, in which there is an intermingling of the hand-ax and Mousterian techniques. McCown interprets this as evidence of the evolutionary transformation of Neanderthal into modern man; but on its face, as well as in the light of the proved antiquity of *Homo sapiens*, it seems much more likely that this mixture of humanities and cultures resulted from hybridization between the two types. This may be but a single example of a process of intermingling that occurred here and there over a fairly long period.

The firstcomers after the Neanderthalers appear to have been relatively small men with long, narrow heads and faces of only moderate breadth and length—such men as might have descended from the man of Galley Hill. Their remains have been found at Combe-Capelle, in France, Předmost, in Czechoslovakia, Brünn (Brno), in Moravia, and elsewhere; the two first mentioned were of the Aurignacian period; the last, of the Solutrian. Men of this type were probably the ancestors of the long-headed peoples that now inhabit northwestern Europe.

Another type of man that seems to have inhabited various places in western Europe throughout the three Upper Paleolithic periods has been called the *Cro-Magnon race.* A typical Cro-Magnon was tall, with long shins and forearms and with large head; the skull was generally long and flattened above, but the face was disproportionately broad and short. There has been a tendency to attribute all the higher developments of plastic and graphic art and the finest Paleolithic crafts exclusively to this "race." More recent studies suggest that, although this was a common type during the Upper Paleolithic cultural periods, there may never have been an actual "Cro-Magnon race" in the strict sense, *i.e.*, a great body of mankind having a majority of identical physical characters inherited from common ancestors. The remains that have been attributed to the "Cro-Magnon race" actually vary widely in almost every respect. Some of these men were exceptionally tall, others quite short; some had long and others round heads; tall, narrow faces were not uncommon. One of the most surprising results of study of the Palestine men of our species is the great amount of variability that they exhibit. Hooton has suggested that, during the late Paleolithic period, immigration of roundheaded, broad-faced men from the East and a less extensive influx of long-headed negroid types from Africa produced in Europe a mixed population based on the original long-headed and relatively narrow-faced stock. Hybridization often results in increased size and vigor, and the broad face and long skull of "Cro-Magnons" suggest recombination of characters from a hybrid mixture.

The "Cro-Magnon race," if it ever existed, has disappeared today, although the peculiar combination of features supposed to characterize it occasionally appears in various human stocks. In any case, there seems no reason to doubt that the modern inhabitants of Europe are largely descendants of these early men, who first came on the scene some 60,000 or more years ago.

The supposed existence of modern types of man in Asia during the late Paleolithic has recently been confirmed in most interesting manner. In 1939, Dr. Weidenreich and Dr. Pei announced the results of investigations made in one of the upper caves at Choukoutien, China—the same place, it will be recalled, where Sinanthropus was found in the lower caves. They found the skeletons of an entire family group that had apparently been killed during a raid by enemies, since the skulls were broken by blows or pierced by sharp instruments. The family consisted of an old man, a younger man, two young women, a child of five years, and an infant, or possibly a fetus. The period when this group lived in the cave was determined by the associated animals and artifacts to have been sometime during the Upper Paleolithic, perhaps 60,000 to 100,000 years ago or even earlier.

This ancient Chinese family was obviously a single group, yet these people show the same interesting mingling of characters observed in their European contemporaries. The old man is quite like European types, but with a strong admixture of Neanderthal characteristics; one of the women has a skull like those of modern Melanesians, the other like those of Eskimos. All of them suggest types common among the American Indians. Here we encounter the same indications of hybridization occurring between wandering groups and causing heterogeneity.

Evolutionary Changes in Man. We may conclude this survey of man's early history by summing up the principal morphological changes that have brought man to his present state from a stage represented by Pithecanthropus or Sinanthropus, and considering certain related topics. Within the million years of the Pleistocene, he has not increased in bulk or much in stature; on the contrary, man is more slightly built than the older types. He has become fully erect, from a once somewhat stooping posture, and now holds his head poised on a relatively slender neck instead of thrusting it forward out of a pair of massive shoulders. His feet have become more fully adapted to walking, and he rests his weight more along the center or toward the inner edge than on the outer edge, as formerly. The skull shows the most important changes, having become much more domelike and capacious, to contain the greatly enlarged brain; at the same time, there has been a reduction in the relative size of the face and jaws. It is interesting to note that the same widening of the face and shortening of the muzzle, with relative increase in the size of the brain case, occurs in dwarf races of dogs produced by artificial selection. The two are not invariably correlated, however, as is proved by the enormous jaw that accompanies the enlarged cranium of Piltdown man. The brow ridges have been largely obliterated in modern man, although in an occasional individual they may be of Neanderthaloid dimensions. The nose, from being flat, broad, and depressed at the base, shows a variable amount of change and in the most advanced form has become narrow and high-bridged; the hawklike profile of extreme Jewish and Armenian types is a highly evolved characteristic.

The teeth have suffered along with the reduction of the jaw. The most modern types of molars have only four cusps arranged in a simple cross pattern, instead of the more complex and apelike 5-cusped pattern of primitive man. The wisdom teeth are rapidly becoming vestigial structures that may cause almost as much trouble as that other leftover, our appendix. Tooth decay, or dental caries, is another of our modern acquisitions. Of 148 teeth and 13 lower jaws of Peking man studied, not one shows any sign of caries, pyorrhea, or other unhealthy conditions. Among large numbers of Old Stone Age remains, more than 100,000 years old, only 5 to 20 per cent show caries; in the New Stone Age, the proportion rises to 15 to 45 per cent; among ancient Persians at about the dawn of history, 75 to 90 per cent of the population had decayed teeth—a proportion as high as that in any modern "civilized" group.

However, in compensation for some of the troubles that have come with the growth of our brains, we live much longer than primitive man did. The approximate age of an individual at the time of his death can be determined by the degree of fusion of the sutures between the bones of his skull. Among the 38 known skulls of Sinanthropus, 15 are of children under fourteen years old, as shown by their possession of milk teeth. Not all the adults can be given ages, but of those that could, 3 were less than thirty years old, 3 were between forty and fifty, and one patriarch was over fifty, perhaps as much as sixty years of age. Among Neanderthals of the Old Stone Age, 55 per cent died before they were twenty, 40 per cent between twenty and forty, and 5 per cent between forty and fifty; none is known over fifty years old. Among the "Cro-Magnons" of 30,000 to 60,000 years ago, 34 per cent died before they were twenty, 53 per cent between twenty and forty, and 10.5 per cent before reaching the age of fifty; of the entire group, only 3 individuals are known that passed the age of fifty, and none of these reached seventy. The story remains about the same in the New Stone Age, and even as late in history as Roman times the record is not much better. It has been calculated that the average Roman under the Caesars lived to be only eighteen years old. Since that time, the average duration of life has been lengthening—very slowly at first but at an increasing rate since the development of scientific medicine. The average duration of life was twenty-nine years in France at the time of the revolution, thirty-seven years in 1850, forty years in 1880, and more than sixty years for men, fifty-four years for women in 1940. Much of this increase is attributable to modern science; but there is also reason to believe that the natural span of life, barring accidents, has been increasing since Stone Age times. In that far-off world, death by violence was the rule, but the rare individual who reached fifty was apparently already approaching senility.

THE HISTORY OF HUMAN CULTURES

Running parallel to the fossil record of man himself is another history—that of the evolution of human cultures. The materials from which this story has to be pieced together are the objects made and used by man, which we call *artifacts.* An assemblage of artifacts at a given locality and of the same age is an *industry;* the sum of the activities of the people, as shown by their industries and other discoverable characteristics, constitutes a *culture.*

Weapons, tools, ornaments, and utensils are lost, or broken and cast aside. Where natural sedimentation is going on, they may be buried like other fossils, the older beneath the younger. On sites that man has occupied for long periods, there is a steady accumulation of debris, giving the same result of stratification. Favored situations, such as caves or natural fortifications, may be occupied at intervals for thousands of years, and the accumulation of debris may attain considerable thickness. In a section through such a deposit, the *sequence* of the cultures is recorded by the buried artifacts of the different levels. As in paleontology, after the relative ages of cultures have been established in such stratified deposits, the cultures themselves may be used to date other sites that have not been so long occupied.

This method obviously has its difficulties and limitations. Within a restricted area, such as Europe, a given culture sequence may furnish an accurate and reliable method of dating. But in widely separated regions with different environments, unlike cultures may exist simultaneously; and under similar environments, parallel types of culture may develop at different times in separated regions. Higher cultures may spread slowly at the expense of simpler ones through migration, commercial contact, or conquest, so that marginal occurrences may be more recent than central ones. Some of the North American Indians were in Paleolithic, some in Neolithic or Chalcolithic stages at a time when Europeans had produced the iron and steel cultures.

Sometimes the type of man responsible for the production of a given culture can be ascertained by finding his skeletal remains together with the artifacts. Thus, Neanderthal man is everywhere associated with the Mousterian culture. Race and culture are, of course, by no means synonymous and in historic times, cultures have spread to men of diverse racial stocks; but evidence is accumulating that among prehistoric men, culture and race had a very strong tendency to remain associated and that even when diffusion of cultural elements occurred, they received the impress of the culture pattern of the group that adopted them. Later, as movement of peoples, density of populations, and commercial and military contacts increased, the rate of cultural diffusion also speeded up, and the association of culture and race has become less close.

Since the history of early man is best known in Europe, the European culture sequence has become the standard for comparison. The accompanying table shows the relation between the Pleistocene stages, the cultural chronology, and the known fossil types of men.

The Eolithic Culture. Eoliths are rudely chipped, variously shaped flints that the most ancient men are supposed to have made before they were skillful enough to make implements of recognizable types. It is admittedly very hard to distinguish them from stones chipped by stream battering, frost action, and the like; many supposed eoliths are probably not such. But no one denies that the earliest implements must have been of this sort. Supposed eoliths have been found in deposits of late Pliocene; and at Ipswich, England, they occur in a layer just beneath another uppermost Pliocene deposit that contains more or less definitely fashioned implements of indubitably human origin. In 1937, W. C. Pei reported the discovery of worked stone and some worked bones in Pliocene deposits of China which are even older than Sinanthropus.

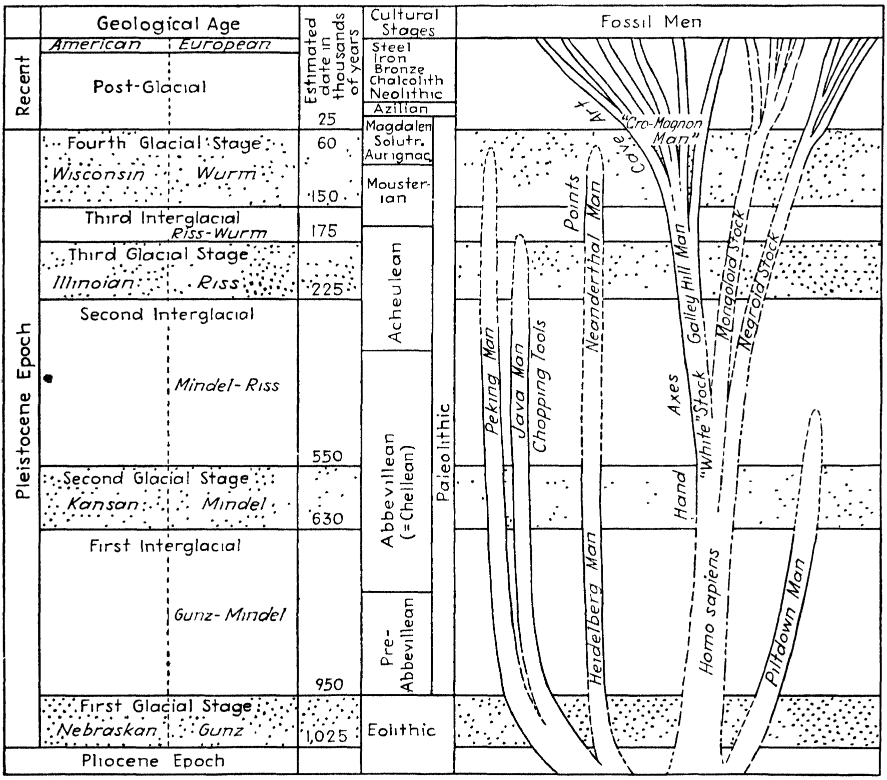

FIG. 138. *Table of human chronology.*

The Old Stone Age

The culture found associated with Peking man may be regarded as a transitional stage between the Eolithic and the Paleolithic cultural eras. Peking man was evidently a hunter, for the Choukoutien cave deposits are full of the bones of his food animals, broken and mostly blackened by fire. He was not, however, solely a flesh eater; great quantities of the small, nutlike oily seeds of the hackberry tree were also found in the deposits, and these evidently constituted one of his chief foods. Besides telling us something of the food habits of this early man, these hackberry seeds show that the China of his day had a temperate climate, and this is further borne out by the finding of a charred piece of redbud wood in one of his campfires. The fact that Peking man knew and used fire shows that he had already taken perhaps the greatest cultural step ever made by man. His stone implements, though so crudely formed that they were not identified for some time after the excavations were in progress, are more than eoliths, being of recognizable types and uses. The most characteristic are chopping tools, made from great flakes of stone or from river pebbles, coarsely chipped to produce a cutting edge. Along with these are found rude scrapers, pointed implements, and bones that had been scratched, grooved and cut—though it is doubtful if the bones are systematically fashioned into tools.

In 1935, von Koenigswald discovered the same types of chopping and scraping tools at Patjitan, in Java, under circumstances that make it almost certain that they were made by Pithecanthropus. Recognition of a type of culture common to Pithecanthropus and Sinanthropus[1] and associated with no other known type of man has made it possible to postulate the occurrence of men of this stock in certain other areas where their remains have not yet been found. In northern India, de Terra has discovered a similar industry, which he calls the *Soan,* beginning at the base of the Middle Pleistocene and extending through the remainder of the epoch. An almost identical industry was found in 1937 in Burma. We therefore are able to visualize the distribution of Java-Peking man half a million years ago as covering a great triangular area of southeastern Asia south of the Himalayas, from northern India to northern China and south to Java. Over the whole of this region, the essential characteristics of the culture remained almost constant for a very long time. Interestingly enough, there is evidence of contact between Java-Peking man and the makers of the hand axes, both in Java and in India. In Java, there have been found a few "imitation" hand axes, imperfectly reproducing their form but not their characteristic technique; and in India, from a center of hand-ax culture in the south, the influence can be traced northward in diminishing amount to the base of the Himalayas and the region of the Soan industry. It is as yet mere hypothesis that the hand-ax makers were men of our own species, as they were in Europe.

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[1] Among the culture traits of these men, a special type of cannibalism is apparently indicated by the fact that most of the skulls recovered have had the basal region purposely knocked out, apparently in order to reach the brain.

Evidence of Old Stone Age cultures is widespread in Europe, Africa, and the Near East, but only the European sites have been thoroughly investigated. These cultures are largely differentiated on the basis of their artifacts, but much can also be learned about the activities of the people who made them by a consideration of the places in which they chose to live, the remains of their food, and the ways in which they disposed of their dead.

The Abbevillian and Acheulean Cultures. In Europe, the oldest recognizable stone implements, with the exception of eoliths, are found in the gravel beds of the higher and older river terraces and in other open-air sites. They are called *hand axes* and are made from flint nodules, chipped on both faces. The older ones are coarsely and rudely chipped, recognizable by their pear shape and sinuous edges and imperfect workmanship. This culture, known as the *Abbevillian*,[1] occurs in the river gravels of the first interglacial period and in those of the enormously long second interglacial. Before the end of that long time of mild climates, the hand ax developed into much better worked, lighter and thinner almond-shaped implements, finely chipped all over, with straight edges, more effective for cutting or chopping. They were made by skillfully detaching small flakes from both sides of a flint core, so that the edge, which is now carried clear around the implement, is now moderately sharp and regular. These Acheulean implements are found in lower and more recent terraces than the Abbevillian and can be traced through various modifications from the middle of the second interglacial through the first half of the third interglacial stage. In their final form, they became small, flat, triangular points. With the hand axes are found various flake borers, blades, scrapers, and points, but the hand ax is the characteristic implement of the culture. As we have already seen, men of the Galley Hill type—primitive members of our own species—made the Acheulean implements and hence, presumably, the Abbevillian ones from which the former developed.

The Mousterian Culture. Superimposed upon the Acheulean implements in some of the river gravels are found tools of an entirely different technique, made by detaching a flint flake from a core and then trimming up one side of the flake by chipping, leaving smooth the side detached from the original matrix. The edges were retouched by pressing off minute flakes with a bone tool. The most characteristic implements are the point—a roughly worked triangular tool that is the prototype of the spearhead and arrowhead—and the side scraper.

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[1] Long called the *Chellean* but renamed because the implements found at Chelles, France, the type locality, have proved to be derived from some earlier deposit instead of being *in situ*.

Mousterian tools found in the gravels are generally associated with a warm-climate fauna, but during the later stages of this culture, the makers inhabited caves, in which implements are found in abundance, with traces of fire and with remains of animals used as food. These are cold-climate animals, including the wooly rhinoceros, the mammoth, and the cave bear, which lived during the last, or Würm advance of the ice sheets. Skeletons found with these implements and bones show that the cave dwellers were Neanderthalers.

The Upper Paleolithic Cultures. All the European cultures based on tools of chipped and flaked flint are grouped as the Old Stone Age, or Paleolithic. The earlier and cruder Abbevillean, Acheulean, and Mousterian cultures make up the lower Paleolithic. With the coming of modern man and the disappearance of Neanderthalers from Europe, there was introduced a series of cultures likewise based on flint tools, but of much finer and more varied workmanship. These characterize the Aurignacian, Solutrian, and Magdalenian periods.

The flint tools and weapons of the *Aurignacian culture* are smaller and more diversified in form than those made by Neanderthal man, and the use of bone tools becomes common. End scrapers, gravers, knifelike blades, and other implements are common and are of beautiful workmanship. Ceremonial burial was practiced, the bodies being often buried in red ocher with implements and ornaments. The beginnings of plastic and graphic art date from this period, as described below.

The bones of animals from the earlier Aurignacian deposits are mostly the same as those of the Upper Mousterian period, indicating a *cold but moist* glacial climate; later there is a great increase in bones of horses, musk oxen, and reindeer, showing that the damp cold of the glacial maximum was succeeded by a *cold but dry* climate like that of the Siberian steppes today. During this stage, the Aurignacians were chiefly hunters of horses, living in great encampments; in one such site, remains of 100,000 horses have been estimated to occur.

The *Solutrian period* coincided with a climatic change marked by an increase in the number of reindeer and a decrease in the abundance of horses. The most characteristic artifacts are finely worked, laurel-leaf-shaped flint blades, often large, very thin, and beautifully chipped, with ripple flaking on both sides. This period forms a break in the culture sequence, for the following *Magdalenian period* appears to be a development from the earlier Aurignacian rather than from the Solutrian. During the Magdalenian period, the climate became so cold that open-air encampments were largely abandoned in favor of caves; the use of bone tools was extended, with the development of skillfully made needles, polishers, harpoons, and bone engravings.

Upper Paleolithic Art. As a part of their attempted magical control of nature, the Aurignacian "medicine men," or wizards, scratched pictures of animals and man on stones and on the walls of their caves. Sometimes the pictured animals were wounded to ensure success in the chase;

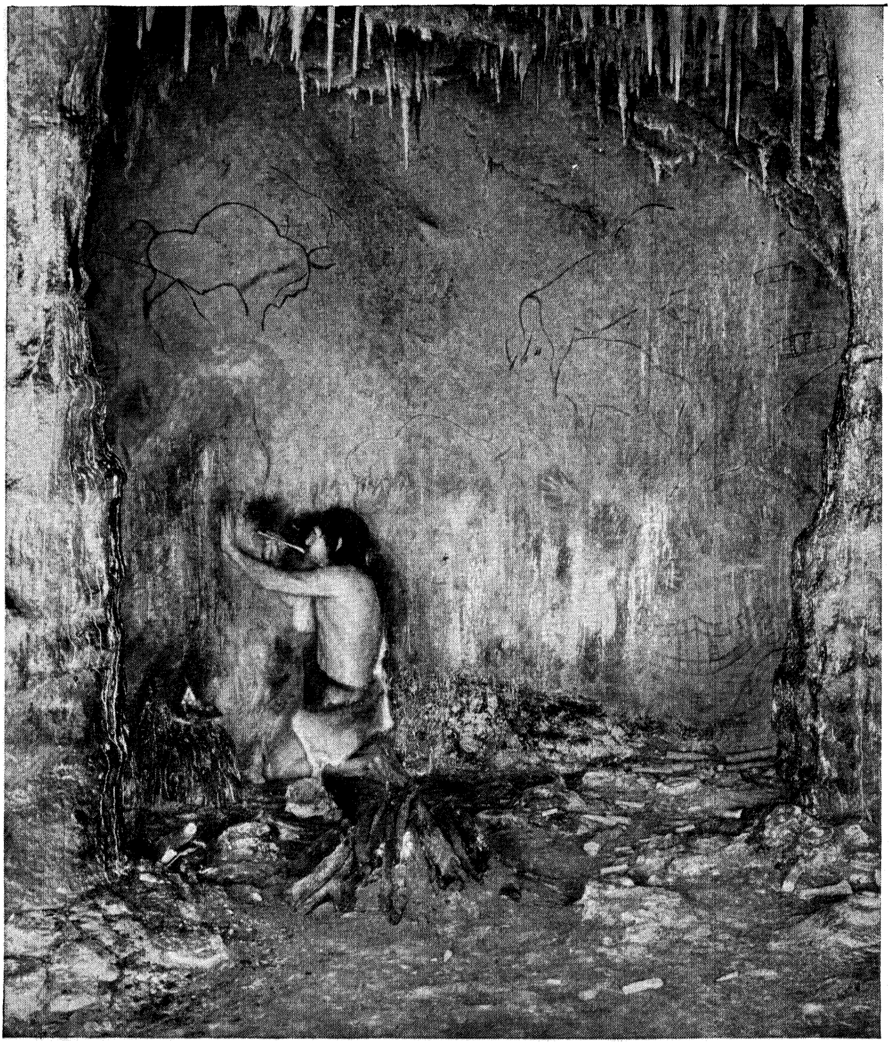
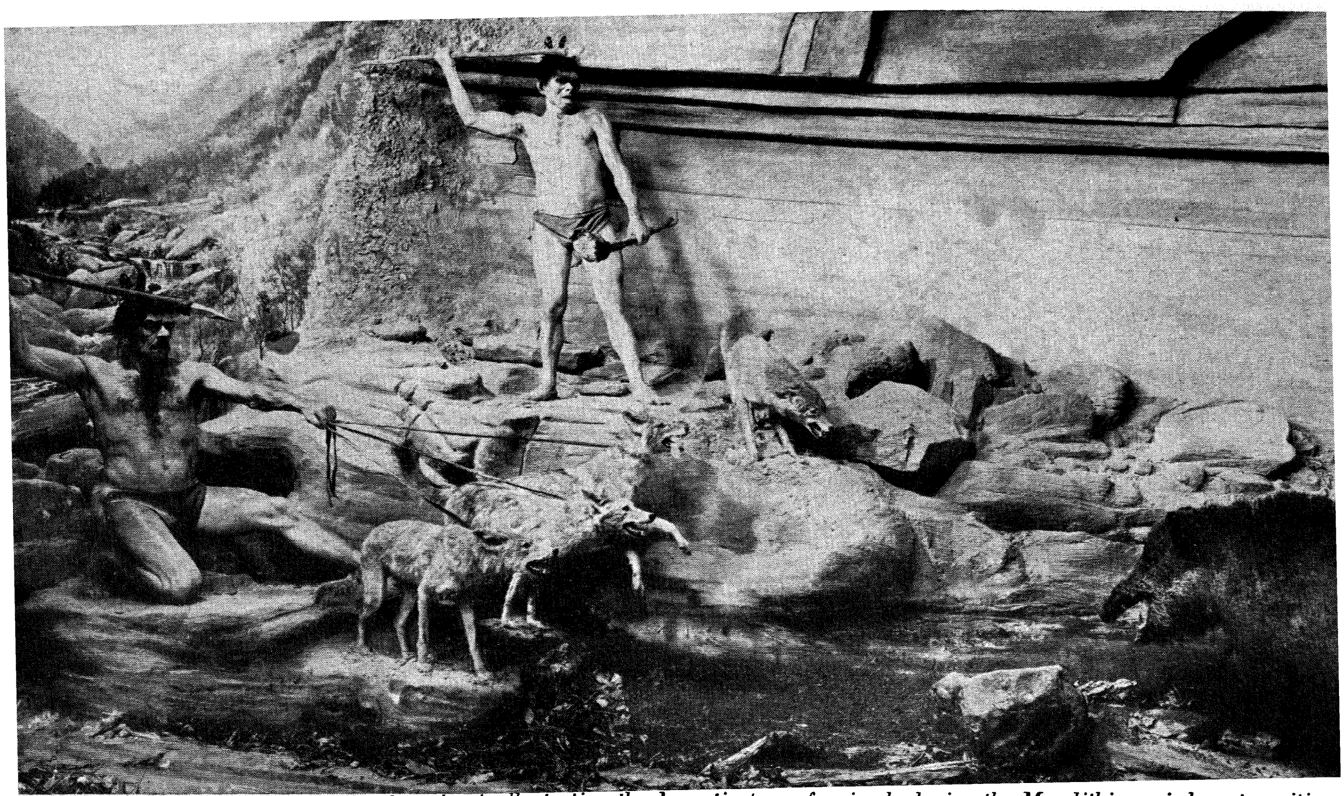


Fig. 139. *Restoration of a Late Paleolithic scene in a cave in France, showing an Aurignacian artist outlining his left hand, pressed against the wall, by blowing powdered red ochre through a bone tube around it.* (*Courtesy of the Field Museum of Natural History, Chicago.*)

sometimes they were shown breeding to ensure abundance of food. At first, the pictures were crude outline sketches, but toward the end of the Upper Paleolithic period, they reached a pitch of artistic excellence not surpassed until thousands of years later. Painting with clay and



IG. 140. *Restoration of an Azilian boar hunt, illustrating the domestication of animals during the Mesolithic period, or transition from the old to the new stone age.* (*Courtesy of the Field Museum of Natural History, Chicago.*)

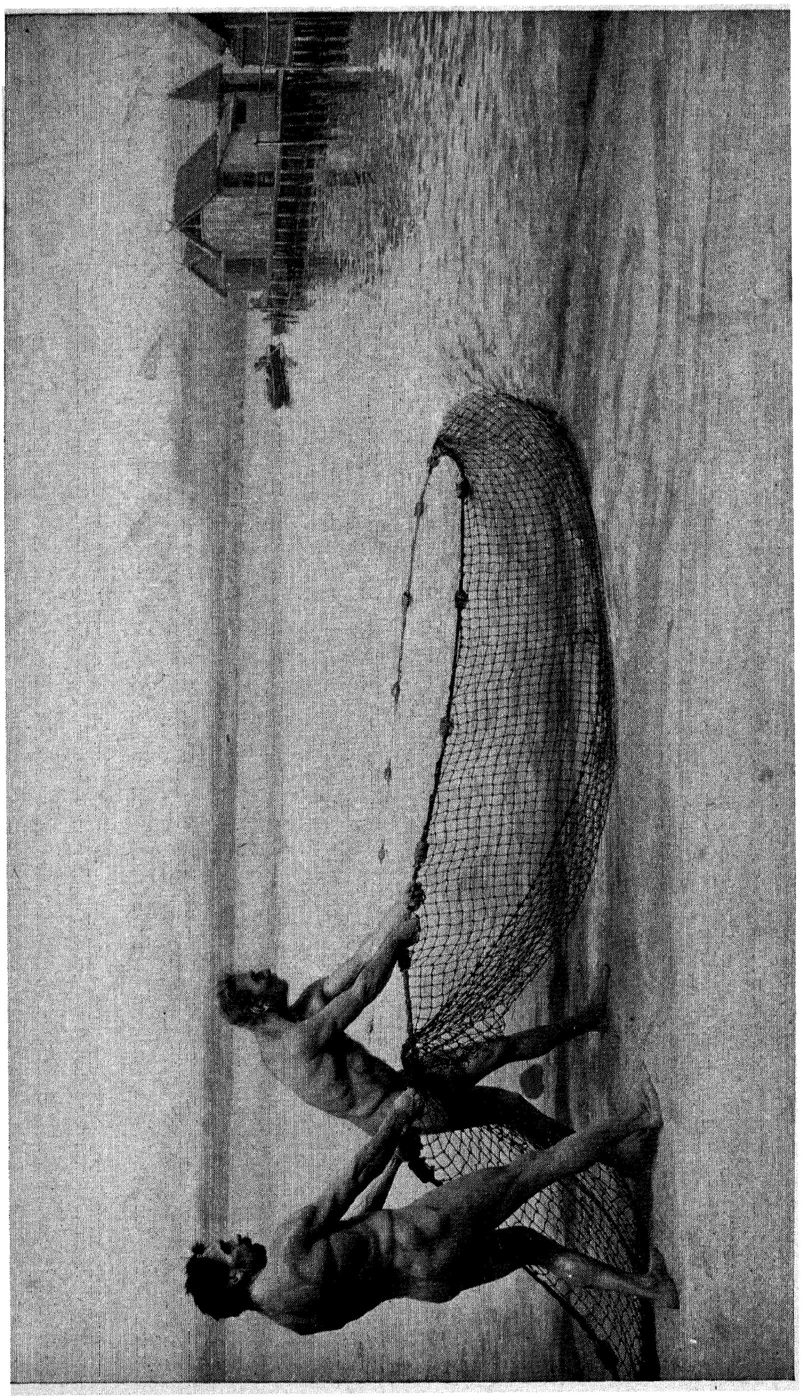


Fig. 141. *Swiss lake dwellers of the late Neolithic (predominantly Alpine in type) haul in their seine at Neuchâtel Switzerland.* (*Courtesy of the Field Museum of Natural History, Chicago.*)

oxide pigments, modeling in clay, and carving in stone were also common. The Solutrian period shows little trace of art and constitutes an interruption in this aspect of Upper Paleolithic culture—another reason for regarding the Solutrian peoples as temporary invaders of a large European population with a different culture, which appears first as the Aurignacian and later as the Magdalenian. Upper Paleolithic art and industry have been attributed largely to the "Cro-Magnon race" but may well have been the work of a number of different racial groups sharing a common culture.

The only record of Upper Paleolithic culture in Asia, outside Palestine, is that of the family that inhabited the upper cave at Choukoutien, China, which we have already discussed. These people possessed a relatively advanced culture, with chipped-stone implements, a bone needle, other bone tools, and necklaces and other ornaments made from beads of perforated teeth, worked stones, and fish and bird bones. They were evidently hunters, since the earth floor of the cave was full of remains of their food animals.

The Azilian Culture. This stage occurred during the transition from glacial times to modern climatic conditions in Europe. The Azilian is a somewhat degenerate successor of the Magdalenian culture. The flint implements and bone tools are smaller and poorer in workmanship, and engravings and paintings of animals are no longer made; but many rounded pebbles are found, painted in red ocher with bars, dots, crosses, and other signs. The Azilian fauna was practically that of modern Europe. A peculiar feature of the culture was the burial of the heads of the dead apart from the bodies. The Azilian and related cultures are sometimes grouped as the Mesolithic, or Middle Stone Age.

The Neolithic and Later Cultures. The Azilian culture was superseded by one in which the stone implements were shaped by grinding and polishing rather than by chipping and flaking. Here we encounter the first evidence of the domestication of animals (the oldest being the dog); and a little later, cultivation of plants was first begun. This is the *Neolithic*, or New Stone Age, and here we approach the dawn of history, for the oldest Egyptian, Mesopotamian, and Indo-Iranian settlements were in this or the upper Paleolithic cultural stages. In Mesopotamia, the Neolithic culture lasted until about 5000 B.C., when the use of hammered copper was introduced, giving rise to the *Chalcolithic*, or stone and copper culture. The Neolithic and Chalcolithic periods saw the development of agriculture and the growth of city-states in the Near East. In this region, the *Bronze Age* began about 3000 B.C., marking the transition from prehistoric to historic times; the Sumerian Empire, the siege of Troy, and the Cretan civilization were events of the Bronze Age. Bronze was superseded by iron; and iron by steel, the basis of modern civilizations.

CHAPTER XXXIII

The Races of Modern Man

Having undertaken to trace the evolutionary history of mankind in some detail, we are now ready to consider briefly the characteristics and distribution of the more important subdivisions of our own species and what is known of their origins and development. Here biology impinges upon history; not only is the racial history of man of interest biologically; it is important also to the student of human affairs, for many of the most significant events in history have resulted from the contacts or interminglings of peoples of diverse ancestry and culture. We have seen that men of our own species originated somewhere in the Old World, though just where or when is uncertain, and that they were already present in Europe in mid-Pleistocene times, some half million years ago. Before the dawn of history, they had spread to all the continents except isolated and inhospitable Antarctica, and had even reached most of the far-flung islands of the Pacific Ocean. Today man is probably the most widely distributed of animal species. Like all such wide-ranging forms, he exhibits marked diversity, which extends to his cultural as well as to his morphological characteristics.

Important though an understanding of racial differences among men is, few aspects of humanity are more misunderstood, more complex, or more difficult to study. To the average person, "race" is an undefined complex of bodily characteristics, cultural phenomena, language, nationality, religion, and geographic location, overlaid with subjective judgments as to mental and moral qualities. The average man uses the term in a variety of noncomparable and often conflicting senses, with first one and then another of the above-mentioned elements uppermost in his mind. Thus he may speak of the "White race," the "Jewish race," the "Latin race," or the "Irish race." The first usage assumes skin color as the basis of differentiation; the second, religion; the third, language; and the fourth, either geographic location or certain peculiarities of temperament.

To the biologist, on the other hand, the criteria of race must be the inherited physical characteristics of men—the variations in such features as hair, skin, nose, eyes, stature, and differences in shape and proportions of the head, trunk, and limbs. Hooton[1] defines a *race* in this sense as being "a great division of mankind, the members of which, though individually varying, are characterized as a group by a certain combination of morphological and metrical features, principally nonadaptive, which have been derived from their common descent." He distinguishes between *primary races,* which have been modified only by the operation of evolutionary factors, including the selection of their own intrinsic variations and of modifications possibly produced in response to environmental stimuli, and secondary, or *composite races,* in which a stabilized combination has been effected by a long-continued intermixture of primary races within an area of relative isolation.

The number of morphological features that may be considered in racial classification is very great, but some are of much more importance than others. In general, nonadaptive characteristics are most useful and reliable. As examples of these, Hooton cites the following:

> The form, color, and quantity of the hair, and its distribution in tracts; the color of the eyes and the form of the eye-lid skin folds; the form of the nasal cartilages, the form of the lips and the external ear, the prominence of the chin; the breadth of the head relative to its length; the length of the face; the sutural patterns, the presence or absence of a postglenoid tubercle and pharyngeal fossa or tubercle, prognathism [projection of the jaws], the form of the incisor teeth; the form of the vertebral border of the scapula, the presence or absence of a supracondyloid process or foramen of the humerus [see page 314], the length of the forearm relative to the arm; the degree of bowing of the radius and ulna; the length of the leg relative to the thigh. Hooton's classification, although simpler than many, is superior to most in that it gives due weight to numerous characteristics found in all parts of the body. Many of these features are unavailable in skeletal material, and this constitutes a severe handicap in dealing with the ancient populations. Of all skeletal characters, the proportions of the skull are the most significant and reliable.

Head form is one of the most widely used of these features. If the maximum breadth of the skull is less than 75 per cent of its length, the skull is longheaded, or *dolichocephalic;* if more than 80 per cent, it is short-headed, or *brachycephalic;* if between 75 and 80 per cent, it is in the middle class, or *mesocephalic.* This measurement is called the *cranial index.*[2] Though subject to a certain amount of environmental modification, it is on the whole a heritable and nonadaptive feature. The longheaded type of skull is the more primitive, the short-headed (often spoken of as roundheaded) type the more advanced, and geologically the more recent. Height of skull and type of nasal structure have also been much used in racial classification, and Dixon[1] makes these, with the cranial index, the main criteria upon which his analysis is based. There is considerable evidence that these features are inherited independently of one another and are little affected by environment.

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[1] In preparing the accounts of fossil men and of modern races given in this and the preceding chapter, much use has been made of Hooton's work, particularly his two scholarly though somewhat facetiously titled books *Up from the Ape* and *Why Men Behave Like Apes.* Material has also been drawn from publications by Keith, Haddon, Dixon, and others.

[2] The corresponding ratio based on measurements of the living, which include the flesh covering the skull, is called the *cephalic index.*

We cannot profitably go further into the details of the morphological criteria of race; but it should be noted that sometimes one, sometimes another of the above-mentioned features may be the most prominent characteristic of a race, whereas the same feature may show no distinguishing peculiarities in the remaining groups of man. In addition to morphological characters, physiological differences also exist that may be of racial significance, though they have as yet been little studied. Such are the variation in relative proportions of the human blood groupings, in age at puberty, in average duration of life, and in susceptibility to specific diseases in different racial groups.

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[1] Dixon, in *The Racial History of Man* (1923), has attempted an analysis of ancient and modern man based upon three principal skull indices, which his studies indicate are but little subject to environmental modification. In his classification, the three chief parameters are the cranial index (D = dolichocephalic, or longheaded, M = mesocephalic, or medium-headed, B = brachycephalic, or short-headed); the length-height index (C = chaemacephalic, or low-skulled, O = orthocephalic, or medium-skulled, H = hypsicephalic, or high-skulled); and the nasal index, based on length and breadth of the nasal structure of the skull or on corresponding measurements of the nose in the living (L = leptorrhine, or narrow-nosed, M = mesorrhine, or medium-nosed, P = platyrrhine, or broad-nosed). Any skull will fall into one of the groups thus defined, and since all combinations of these characteristics occur, 27 different categories are created. Of these, Dixon recognizes the following 8 as the primary or fundamental types, all the others being assumed to show blending due to intermixture:

D-H-L = Caspian type
D-C-L = Mediterranean type
D-H-P = Proto-Negroid type
D-C-P = Proto-Australoid type
B-H-L = Alpine type
B-C-L = Ural type
B-H-P = Palae-Alpine type
B-C-P = Mongoloid type

Dixon's somewhat artificial scheme lends itself to the statistical analysis of populations and leads to interesting results but is based on too few characters and demands certain assumptions that seem inherently improbable—such as that there were 8 primary groups (the exact number required by the combinations of the extremes of each of the indices) and that all intermediate types have resulted from admixtures of the primary types.

One of the most widely followed classifications is that of Haddon (*The Races of Man,* 1925), based primarily on hair form (Ulotrichi = woolly-haired = Negroids; Cymotrichi = wavy-haired = Whites; Leiotrichi = straight-haired = Mongoloids), subdivided by stature, skin color, and nasal form into 34 racial types, with additional subordinate groupings.

All modern variants of man are regarded as belonging to a single species, *Homo sapiens*, our first glimpse of which is furnished by the man of Galley Hill, who lived in England about 500,000 years ago, during the Middle Pleistocene. There is reason to believe that even at that far-off time, true man was widely distributed in the Old World, coexisting with more primitive human species in Europe, Asia, and Africa. The basic European type seems to have been a short-statured, longheaded man of the White group. We have no certain evidence as to the place or time of origin of any of the three great primary groupings, the Whites, Mongoloids, and Negroids. All three of these probably, and the two latter certainly, developed somewhere outside Europe, and the Negroids and Mongoloids, like the Whites, were already in existence by middle or late Pleistocene. We shall here briefly outline Hooton's classification of the modern races of these stocks and some of their combinations. In giving the characteristics of the various groups, the most significant and reliable features are usually placed first.

THE WHITE RACES

The general characteristics of this group of peoples include the following: skin light brown ("olive"), pale white, or ruddy; facial profile straight; nose usually high and narrow, sometimes medium, the opening into the skull narrow; hair fine or medium in texture, that of the body usually abundant; lumbar curve pronounced and pelvis very broad; hair form prevailingly wavy or straight; female breasts usually hemispherical and female buttocks prominent. This group includes the Mediterranean, Alpine, Nordic, Armenoid and Ainu races and the Dinaric, East Baltic, Arab, Berber, Celtic, and Beaker subraces.[1]

The *Mediterranean race* is probably the least specialized and oldest of the White group. Its people are longheaded, with black or brown, wavy or curly hair and brown eyes. Their faces are symmetrically oval and rather narrow, with narrow noses and lips of medium fullness. They are generally short and slightly built and are usually olive-skinned. To this race belong most Egyptians, Northwest African Berbers and Arabs, southern Italians and Sicilians, Spanish, and Portuguese. Since the dawn of history, the Mediterraneans have formed the chief constituent of the populations of northern Africa, south to the southern edge of the Sahara and the upper reaches of the Nile. These north

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[1] The best and fullest treatment of the White races will be found in Coon, *The Races of Europe*, Macmillan, 1939. This most interesting book, a successor to Ripley's classical study of the same title, presents a somewhat different and very much more elaborate classification of the White races than that here given. Particularly noteworthy are Coon's interpretation of the relations of the older species of man to *Homo sapiens*, which in general agrees with that of Keith and Hooton, and his extensive photographic supplement illustrating racial types.

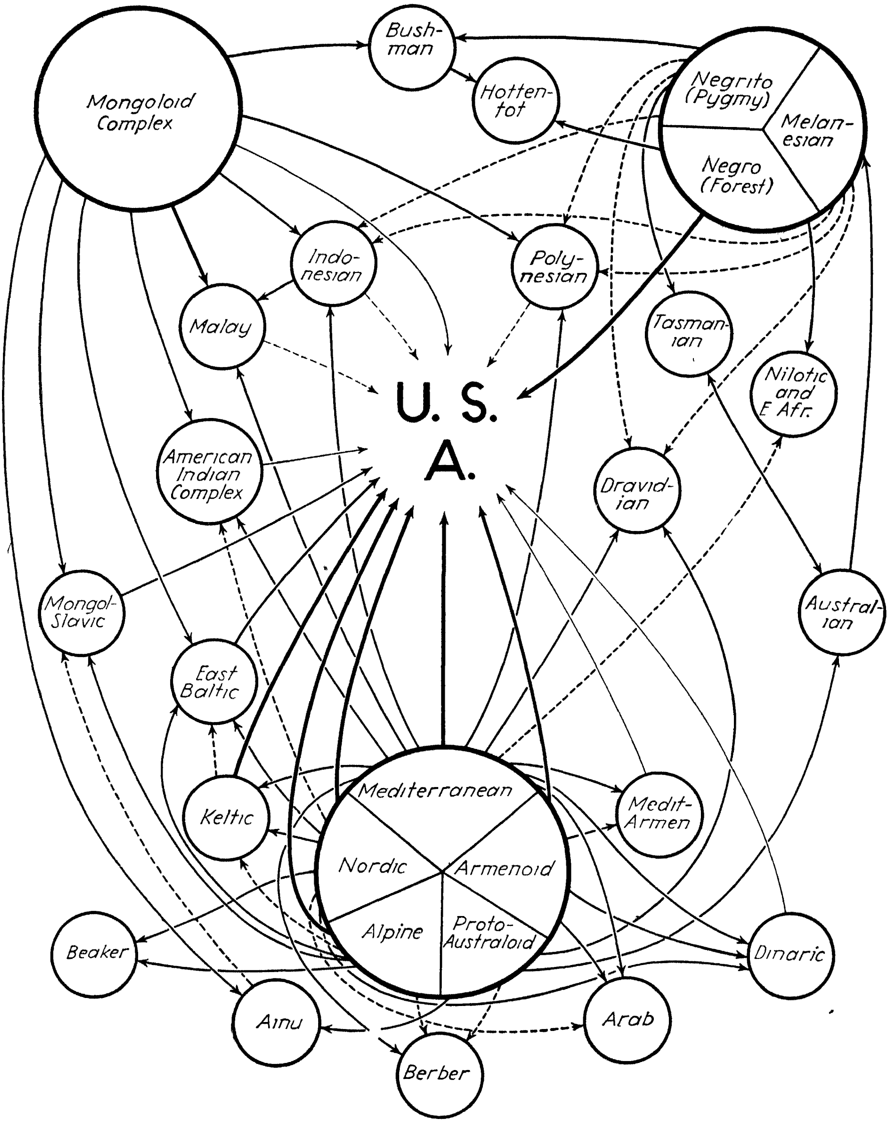
Bush-man
Mongoloid Complex
Hotten-tot
Negrito (Pygmy)
Melan-esian
Negro (Forest)
Indo-nesian
Poly-nesian
Malay
Tasman-ian
Nilotic and E Afr.
U. S. A.
American Indian Complex
Dravid-ian
Mongol-Slavic
Austral-ian
East Baltic
Mediterranean
Keltic
Medit-Armen
Nordic
Armenoid
Alpine
Proto-Australoid
Beaker
Dinaric
Ainu
Arab
Berber

FIG. 142. *A diagram showing the relationships of the principal races of man, and the chief constituents of the population of the United States.*

African peoples were in part known to the ancients as *Libyans*. In central and northeastern Africa, Mediterraneans mixed with Negroid stocks, giving rise to "Hamitic" peoples, represented today by such tribes as the Galla, Somali, Masai, Bahima, and others. In Europe, Mediterraneans, or a somewhat more robust proto-Mediterranean stock (called by Haddon *Eurafricans*), were already present in Aurignacian times, and Galley Hill man of the second interglacial period may have been a member of this race. During the Neolithic period, the Mediterranean race predominated over all Europe, but since then it has been increasingly crowded out by the Alpines, Nordics, and Armenoids, with whom, however, it has mingled. Eastward, the Mediterraneans were present in Egypt and Mesopotamia at least as early as 5000 B.C., founding some of the earliest civilizations; and at some very early period, they spread into India, southeastern Asia, and the Malay Archipelago, contributing to the Dravidian and Indonesian-Malay races. The earliest longheaded migrants into the New World probably brought with them diluted strains of this stock. Where the Mediterraneans originated is uncertain, although northern Africa seems most likely.

The *Nordic race* is typically characterized by the golden or ash-blond hair, blue or sometimes gray eyes, and prevailingly long skull. The face is long and narrow, with a long, high, narrow nose, usually thin-tipped, with compressed nostrils; the mouth is thin-lipped, the upper lip being unusually long. Very commonly there is a fold of skin overhanging the outer corner of the eyelid, unlike the Mongoloid fold that overhangs the entire eyelid or its inner corner only. Men of this race are generally tall, of slender build, with sloping shoulders, shallow chest, relatively short trunk, slender waist, and long legs, especially the shins. The hair is straight or wavy, and there is a strong tendency to baldness in males. Typical peoples of this race are the upland Swedes and Norwegians and many North Germans, English, and Scotch.

Little is known of the Pleistocene history of this vigorous race, which in many respects closely resembles a stronger and more bleached development of a Mediterranean stock. It may have originated around the Baltic, where it now chiefly occurs. Certainly by the end of the Neolithic period the population of Scandinavia, North Germany, and the eastern Baltic lands was predominantly Nordic, and the race also occupied Poland, Czechoslovakia, and a belt stretching eastward across Russia. Its widest distribution seems to have been reached between 5000 B.C. and 2500 B.C., and Nordic invasions of Egypt and northwest Africa have left traces in the blond, longheaded types found among the Berbers and Canary Islanders. There is also reason to believe that at one time the stock reached Central Asia; and the Aryan-speaking peoples that invaded India about 1500 B.C. seem to have been a mixed Nordic and Mediterranean stock.

Before the end of the Neolithic period, the Nordic race was migrating southward, eastward, and westward from the Baltic center. Some of them, mixing with Alpines somewhere in Europe, formed the *Beaker folk*, or *British Bronze Age subrace*,[1] that invaded the British Isles about 2000 to 1800 B.C. and built there the "round barrows." Another Bronze Age Nordic-Alpine group seems to have made up the Achaean peoples who overran the Greek peninsula. At the end of the Bronze Age, about 1100 B.C., similar mixed races that had learned the use of iron in the Austrian Tyrol or in central Europe once more invaded Greece, where they were known as the *Dorians;* and others carried the iron culture into Italy. This was merely the beginning of a long series of such migrations and invasions. During the early part of the Iron Age, Nordic-Mediterranean-Alpine groups seem to have evolved or adopted the Celtic language, and were known to the ancients as *Celts*. They invaded the British Isles many times between 2000 B.C. and the Roman conquest, A.D. 85. The first wave consisted of the Gaels, the second of the Brythons, largely Alpine in race; later came the Belgae, prevailingly Nordic in type. The Gaelic tongues spoken in Ireland, the Isle of Man, and Scotland date back to the first invasion; the Welsh, Brittany and former Cornwall dialects, to the second. The Celts had established themselves in France by 700 B.C., in Spain by 600 B.C. We now approach historic times, and the later movements of mixed Nordic-Alpine peoples are better known. The Teutons, Cimbri, Goths, Vandals, Alemanni, Bavarians, Visigoths, Franks, Angles, Saxons, Jutes, Danes, Norsemen, and Normans, all of whom played their parts in European, Roman, and British history, were largely of this mixed stock, though in some Nordic, in others Alpine strains predominated, and some groups showed Mediterranean admixture.

The *Alpine race* has clearly entered Europe from some other region, at a fairly late date. The men of this race have short, round heads, with broad and rather short faces and often square jaws; their hair is black or brown, oftener straight than wavy, and abundant, with heavy beard; the nose is usually fleshy and short. Alpines are usually of short or medium stature, and their build is thickset, with a short, thick neck, broad shoulders, deep chest, and short, thick arms and legs. Their skin varies from olive to brunet white, rarely pale. Typical modern peoples of this stock are the Czechoslovakians, many Bavarians, and many southern Slavs and Russians.

The ancestors of these short-headed people began to appear in Europe late in Paleolithic time and by the Mesolithic period, some 10,000 years ago, were present in south Germany and in Portugal. During the course of the Neolithic period, they established themselves in many places in Europe, particularly in the Alpine highlands and in the Balkan peninsula. At this same time, they were also present in France, in Denmark, and in various parts of central and southeastern Europe but were not usually the predominant element in the population. They are believed to have been responsible for the spread of the Bronze culture up the Danube and thence to northern and western Europe, but unfortunately their habit of cremating the dead makes it very difficult to trace the details of their history. Their custom of cremation spread to others of the Neolithic peoples and tends to blot out the history of this very interesting period, during which the mingling of Nordic, Mediterranean, and Alpine peoples gave rise to composite races that were of later historic importance. Cremation continued to be practiced throughout the early Iron Ages and during the Roman period, to the detriment of archeology.

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[1] Most recent authorities regard the Beaker Folk as more Dinaric than Nordic in type.

Some things about this race are clear, however. One is that its original home was somewhere on the Asiatic steppes or on the western slopes of the Himalayas and that massive waves of Alpine peoples thence moved westward into Europe over a long period, extending into historic times. The invasions of the Huns, the Bulgars, the Slavs, the Avars, the Hunagars, the Magyars, and various Turkish tribes reinforced the original Alpine stocks and have left eastern and central Europe overwhelmingly brachycephalic today, though originally this region was populated by longheaded peoples. Not all, and perhaps none, of these Asiatic invaders in early historic times were of pure Alpine stock; they were mixed with Mongoloid blood, and the Huns may have been wholly Mongoloid.

Another thing that we do know about the Alpines is that they mingled extensively with Nordic groups, as we have already seen. In the Baltic region the product of this mingling was the "*East Baltic*" *subrace*, with the body build of the Alpine but the skin, hair, and eye coloration of the Nordic. This type is represented by many of the Finns, Latvians, Esthonians, Lithuanians, and Baltic Russians and may be present in Poland. It also shows traces of Mongoloid intermixture.

The *Armenoid race* is characterized specially by the peculiar nose, which is typically convex, high-bridged, long, and often rather wide; the tip is thick and depressed, with the nostrils recurving, and the nasal profile is continuous with the slope of the forehead. This is the most highly specialized nose found in any of the human races. The Armenoid peoples are brachycephalic, with a very high head, rising to a point far back, with a very flat occiput and usually a sloping forehead; the face is long but also broad, with somewhat prominent cheekbones and a rather small jaw with a moderate chin; the lips are full, the lower everted. The hair is black or brown. usually wavy but sometimes curly or straight, abundant on the head, face, and body, the eyebrows thick, meeting above the nose; the eyes are brown, and the skin olive or brunet white. Armenoids are of medium stature, prevailingly thickset, but quite variable in build. Typical peoples of this group are most Armenians, Turks, and Syrians, many Persians and many eastern (Ashkenazim) Jews.

This race has its center of distribution in the Anatolian and Iranian plateaus in western Asia. Nothing is known of its origin or prehistoric beginnings, and our acquaintance with the stock begins with the pictured representations of Sumerians of the fourth and third milleniums B.C., many of which are equipped with the typical Armenoid nose. Babylonian, Assyrian, and Hittite monuments show the prevalence of this race in Anatolia and Mesopotamia throughout historical antiquity, and it seems probable that these were the regions in which the Armenoids arose. From there they spread south to Arabia and east as far as India but apparently did not reach Europe prior to the Iron Age. About 700 to 500 B.C., however, this stock migrated into the Balkan peninsula, Greece, Italy, and possibly other areas. The Etruscans of northern Italy were almost certainly Armenoids who settled there about 800 to 700 B.C.

It was probably during the early Iron Age that there was formed in the present Balkan area, by mixture of Armenoid with Alpine and Nordic types, the *Dinaric subrace*, which now dominates that region. This group of very tall men with Armenoid head form has a less convex nose than the typical Armenoid, its tip being also less fleshy and compressed; the face is longer, the lower jaw heavier, and the chin more prominent than in pure Armenoids; the skin color is somewhat lighter, and blue eyes are common. A large proportion of the Rumanians, Bulgarians, Serbs, Croats, Albanians, Montenegrins, Greeks, and Austrians of the Tyrol region belong to this stock. The Dinaric subrace has doubtless been reinforced in its Armenoid characters by the Turkish invasions of the area during historic times. With the dispersion of the Jews, Armenoid stocks are now found in all European and American countries, with concentrations in the urban centers.

The *Ainu race* is an isolated stock of the White group, aborigenes of Japan, now restricted to the northern islands. They are apparently the remnants of an ancient brunet white or brown stock that may have reached across Asia into European Russia. Their most noteworthy characteristic is the profuseness of the body hair and the heavy beards of the males. The Ainu have undergone recent mixtures with Mongoloid stocks, but many of them are almost indistinguishable from bearded Russian peasants, who may have a good deal of the same blood. They also share some resemblance with the natives of Australia, which may result from the common possession by both of an archaic White racial element, the *Proto-Australoid,* which is strong in the Ainu but in the case of the Australians is heavily mixed with a Melanesian (Oceanic Negro) strain.

Besides the primary White races described above, there are many admixtures of these types, some of which have been mentioned. A mixture of Nordic and Mediterranean stocks is represented by the *Celtic subrace,* a variety of man in northwestern Europe characterized by tallness and dolichocephaly, combined with dark hair, light or medium skins, and either brown or blue eyes. This group is especially common in southern Ireland, somewhat less numerous in the Scottish Highlands, common in England and Wales, and sporadic in France and Spain. The *Berbers* of North Africa are a mixture of Mediterranean with a short-headed, brunet-skinned stock that may be related to the Alpine. The *Arab subrace* is probably based on a Mediterranean stock mixed with a narrow-nosed type; it is very close to the Nordic in body form but probably has an admixture of Armenoid blood. The nose is aquiline and very narrow, with a thin tip, a high bridge, and compressed nostrils; the hair is black or dark brown, wavy or curly; the eyes, black or dark brown; and the skin, brown or olive. The subrace is concentrated in Arabia and north Africa and is sporadic in Spain and southern Italy.

THE NEGROID RACES

This group of races is characterized by the woolly or frizzly hair, the pronounced facial protrusion, the black or dark brown skin, the low, broad, and short nose with flaring nostrils and broad opening into the skull, the thick, puffy, and everted lips, the poorly developed calf of the leg, protruding heel, and low foot arch, the prevailingly longheaded skull, with marked protrusion of the occiput, the dark brown or black eyes, the long forearm relative to the arm, the short thumb, the coarse and wiry texture of the hair, which is short on the head and sparse on the body and face, the usually conical female breasts, the buttocks less projecting than in females of the White races. This group of peoples includes the Negro, Melanesian and Negrito races, and the Nilotic and Tasmanian subraces. Ancient and specialized, the Negroid races are concentrated in two widely separated areas of the Old World—tropical Africa and Oceania. The Negroes proper are in Africa, the Melanesians in the New Guinea region, and the pygmies or Negritos in both areas.

The Negro race occurs in two chief types. One, the *true,* or "forest," Negro, is found along the coast of West Africa from the Senegal River south to the southern boundary of Portuguese West Africa, inland in the Niger basin, and in the eastern lake region. These people have an extremely protrusive face, a broad, flattened nose, puffy and everted lips, a heavy trunk, long arms, and relatively short legs. The second type, the *Nilotic Negro,* occurs about the headwaters of the Nile and also in the lake region. It is a very slender, straight-faced stock, with tremendously elongated legs and very tall stature, averaging 6 feet to 6 feet 2 inches in height. This group shows traces of Mediterranean mixture.

There is evidence that Negroes have been in Africa since sometime during the Pleistocene and that some mixing with Mediterranean peoples has occurred; but pure Negroid stocks seem never to have been present in Europe in either prehistoric or historic time. On the other hand, there is ample evidence of their former presence throughout most of southern and southeastern Asia, as shown by the Negroid characteristics that appear in the populations of parts of Mesopotamia, central and southern India, Assam, and the hill folk of Burma. They may even have extended north into central Asia in prehistoric times, since there are traces of Negroid intermixture in the peoples living along the Chinese-Tibetan border.

The *Melanesian race* includes the Oceanic Negroes who inhabit New Guinea, New Caledonia, and Fiji. The peoples occupying the smaller islands and parts of the New Guinea coast speak the Melanesian languages; those in the interior of New Guinea, on the remainder of its coast, and on a few of the smaller islands speak the Papuan tongues. Both these groups probably came from a single stock. They are distinguished from the African Negro by the less projecting face, thinner lips, more frequently convex and (in the Papuans) often hook-tipped nose, heavier brow ridges, and more depressed nasal roots. Their hair form is more frizzly than woolly. Some mixture with non-Negroid strains has almost certainly occurred.

The *Negritos* are the smallest of men, males averaging 4 feet 9 inches in height. In this they are approached only by the Tasmanians and some of the "Black-fellows" or "Bush-fellows" of the eastern coast of Australia, who possess a large share of Negrito blood. These Pygmies in most respects resemble the Negroes fairly closely, most of their differences suggesting infantilism—narrow shoulders, short legs, potbellies, bulging foreheads, and relatively short skulls. Their distribution, like that of the larger Negroids, is highly discontinuous. They occur in the Congo forests of Africa, in the interior of New Guinea, in the Malay Peninsula, the Andaman Islands in the Indian Ocean, and the Philippine Islands. This distribution suggests that they once occurred all along the southern edge of Asia, prior to the arrival of the larger Negroid peoples, and that with the coming of the latter, they disappeared, except where they were able to retreat into the inaccessible places that they occupy today. Their origin is a mystery that has caused much speculation.

THE MONGOLOID GROUP

The Mongoloids are a racial complex that cannot at present be satisfactorily broken up. They are characterized by the following features: eyelid with a Mongoloid fold which, when the eye is open, either conceals the edge of the lid along its whole extent or on the side toward the nose (giving the "slant-eyed" effect associated with this race); skin yellow or yellowish brown; hair black, straight and very coarse, sparse on face and body, very long on head; face very broad, with projecting cheekbones and square jaws, nose very low at the root, bridge very low and of medium breadth, concave, with elevated tip and moderately flaring nostrils; eyes dark brown or brown; usually roundheaded and low-crowned, but head form variable; stature prevailingly medium or short, build squat, with broad shoulders, long trunk, short legs, and arms of medium length; breast form in female prevailingly disk-shaped. The distribution of this race is northern, central, and southeastern Asia. In purest form, the Mongoloid type is represented by the Mongols, Tungus, Buriats, and Kalmucks; it also occurs in more mixed form among the Chinese and Japanese, especially in the north Chinese, Manchus, Koreans, etc.

There can be no doubt that the Mongoloids arose somewhere in central Asia. Suggestions of Mongoloid characteristics are contained in the skulls of some of the individuals found in the Upper Paleolithic cave at Choukoutien, which we have previously mentioned, and similar hints of the existence of this race are found in some Upper Paleolithic skulls from Europe. These are probably marginal diffusions of the type. The original center of this short-headed race was probably on or near the central Asiatic plateau, where it seems to have been surrounded on the north, east, and south by longheaded peoples. There is some evidence to show that the Mongoloids must have developed before the end of the Pleistocene epoch but that they did not reach eastern Asia or America until late prehistoric times. The earliest immigrants to the New World were longheaded, with few suggestions of the Mongol stock.

When the race finally began to spread out, it moved eastward, northeastward, and southward. In southeastern Asia, the Mongoloids mixed with longheaded primitive stocks of the White group and with Negroes and Negritos, to give rise to many composite stocks. One of these blends was the great race which has been called the Indonesian-Malay. Mixtures of this composite race with Oceanic Negroid components ultimately produced the Polynesian race, which at a late period passed through the Malay Archipelago and Melanesia and peopled the islands of the far Pacific. Another Mongoloid group followed the original longheaded migrants to America across the Bering Straits, to give rise to the Amerindian races. Finally, in early historic times, there was a great outpouring of Mongols westward in a series of invasions that penetrated Europe and the Near East.

THE COMPOSITE RACES

This group of races includes those compounded of White, Negroid, and Mongoloid elements, or of archaic racial elements unrepresented in their pure forms and surviving only in mixtures with the main modern groups. It has no characteristics common to all its stocks except dark skin pigmentation, dark eye color, and dark hair color. Other composite types, the elements of which are all members of the same racial group, have already been discussed as subraces under the White and Negroid divisions. The principal composite races that involve two or more of the main racial groups are the Australians, the Hamitic- and Bantu-speaking Negroids, the Bushmen and Hottentots, the Dravidians, the Indonesian-Malay peoples, the Polynesians, and the American Indians.

The *native Australians* are an extraordinarily primitive race, both physically and culturally. They have chocolate-colored skins, wavy or curly black hair, plentiful facial and body hair, thin legs, and long, narrow skulls with receding foreheads, heavy brow ridges, protrusive jaws, and broad noses with a depressed root. They are believed to represent the largest element surviving in any race of a very ancient, probably White stock (the Proto-Australoid race), mixed with a Negroid strain. In the southern part of Australia, the hair is wavy rather than curly and never woolly or frizzly, and here children sometimes have reddish or even blond hair and bluish eyes, even where there has been no chance of intermixture with recent European settlers. In the north, on the other hand, evidences of Negro intermixture are clear, the skin being darker, the hair more curly, and the nose even flatter. It is thought that the ancestral stock that gave rise to this race passed through the Malay Archipelago and through Melanesia, perhaps while land connections existed, and that those who remained in Melanesia were absorbed into the later Negro populations, giving the latter the large brow ridges and depressed nasal root found in many Melanesians and Papuans today. Most of the archaic Proto-Australoid race passed on into Australia, there mixing with the primitive Negroids who had already reached that continent. In Australia, the early Negroid population was swamped by the newcomers, darkening the skin and increasing the prognathism of the latter; but in Tasmania, the original Negroid or Negrito stock received but little of the Proto-Australoid strain, and the result was the composite Tasmanian race, which became extinct in 1879.

The mixed Mediterranean-Negroid "Hamitic" peoples of northern and northeastern Africa have already been mentioned in discussing the

Mediterranean race. Southward in the highlands of eastern Africa one can trace a transition in physical type, from Hamitic and Nilotic Negro groups, through tribes such as the Massai, showing various mixtures of these elements, to the great series of *Bantu-speaking Negroids* that occupies much of the Lake District, the east African plateaus, and the southern steppes. The "Bantus" are divided into a large number of tribal groups, from the Baganda in the north around Lake Victoria, to the Zulu and Kaffir of the south, and so through the Betchuana and Barotse to the Herrero of former German Southwest Africa. Although these populations show a varying degree of admixture with some ancient "White" long-headed stock similar to the proto-Australian, they are preponderantly Negroid in type, with moderate to tall stature, brown to black skin, woolly hair, broad noses, and thick lips. Some, like the Zulu and Herrero, have relatively high-vaulted skulls, but in the rest a low-vaulted skull prevails.

The dwarfish *Bushmen* of South Africa exhibit a peculiar mixture of Negroid features—black, kinky ("pepper-corn") hair, broad nose, and full, everted lips—with other characteristics that to some have suggested a partly Mongoloid origin. Particularly noteworthy in this respect are the yellow skin, narrowed and somewhat slanted eyes, and very prominent cheek bones. They are certainly a very distinctive subdivision of mankind, possessing in addition to their other features a racial peculiarity of their own in the enormous development of the buttocks of the women and certain peculiarities in the female genitalia. Dixon and Hooton regard them as the product of a Negroid-Mongoloid cross, and the latter has suggested that they may have originated somewhere on the outskirts of the central Asiatic highlands as the result of contact between Negrito and Mongoloid groups. Other students regard them as wholly Negroid —an ancient and specialized offshoot from this stem whose resemblances to Mongoloid types are mere parallelisms. We know from cave drawings that this hunting people has been in South Africa for at least 15,000 years, and certainly the race has left no traces elsewhere, unless the two skeletons found at Grimaldi, Italy, and the Upper Paleolithic figurines with greatly accentuated buttocks found in parts of Europe may be attributed to it. The Bushmen seem once to have spread over the larger part of British South Africa as far north as the Zambezi River, but they have been driven north and west into the Kalahari Desert and other unfavorable regions by the advance of the "Bantus" and *Hottentots.* The latter people are about intermediate in type between Bushmen and Bantu-type Negroids and probably represent a hybrid population formed through absorption of Bushmen by invading "Bantu" groups.

The highly composite and diversified race that inhabits India is in a broad sense, called the *Dravidian.* This group of peoples has been formed in an ancient "melting pot." The earliest inhabitants of India (excluding the Pithecanthropus-Sinanthropus stock) are believed to have been Negritos, or at any rate some very short Negroid type. With them mixed the archaic Proto-Australoid, possibly "White" race; whether men of the latter stock were the makers of the Indian hand axes can only be surmised. This mingling produced the pre-Dravidian type, which appears to show a mixture of Negroid or Negritoid with Australoid features, having the black skin and small stature of the former and, in some groups, the wavy or straight hair of the latter. Remnants of this stock are still represented by the "jungle tribes" of southern India and the Vedda of Ceylon. Still later, there was an influx of large numbers of Mediterranean Whites, who mingled with the pre-Dravidian stock to produce the present highly composite type of the South Indian Dravidian race. The effect of this last addition was to straighten the face, narrow the nose, further straighten the hair, and perhaps to lighten the skin. In northern India, in later times, immigration of Nordics, Armenoids, and Mongoloids has resulted in mixed types that are scarcely susceptible of classification.

The *Indonesian-Malay race* has already been mentioned in connection with the Mongols. It is the chief group present in the Malay Peninsula and Malay Archipelago but also includes many of the people of Indo-China, Korea, and Japan. The *Indonesian subrace* is shorter, somewhat longer-headed, has wavy hair and less Mongoloid features, a longer and narrower nose, and straighter eyes. The *Malays proper* show much stronger Mongoloid influence. Generally speaking, the Indonesian type occurs inland in the Malay Archipelago, and the Malays are the coastal peoples. The details of the successive migrations that peopled the islands are complex and not too certainly established, but the general outline of events is clear. The first waves included the Negritos, followed by the Proto-Australoids, followed by taller Negroids. Later came a wave of a Mediterranean stock, followed by Mongoloids. These last two, mingling with each other and with Negroid elements, eventually became the Indonesians, who displaced the earlier comers into the interiors of the islands whenever they did not absorb or exterminate them. Finally, the Malays, themselves a mixed stock composed of Mongoloid and non-Negroid components, descended upon the islands, driving the Indonesians, in their turn, back from the coast into the interior.

In the Philippine Islands, for example, there are today some 30,000 to 40,000 "Aeta," or *Negritos*, together with about 50,000 "hill people," who possess a large amount of Negrito blood. All these are wandering tribes of hunters who live in the most inaccessible forested parts of the islands. A second zone of population consists of the so-called "wild tribes"—the Bontocs, Igorrotes, Ilongots, Ifugao, and other formerly head-hunting peoples who live in the mountainous districts and grow rice under great difficulties on terraced hillsides. These are *Indonesians.* All the rest of the Philippine peoples are *Malays,* who occupy the fertile lowlands and make their living as much from the sea as from the land. They represent the last of the prehistoric migration waves.

The *Polynesians* show a mixture of all three of the main racial groups. In some, Mongoloid traits predominate; in others, Negroid; and in still others, there is an approximation to European types. The majority show a harmonious blending of features into a distinctive and easily recognized type of man. There is no obvious predomination of characteristics derived from any one primary group. Whether this result has come from a hybridization that occurred before the migrations that peopled the islands or from successive waves of emigrants of different stocks is yet to be determined.

The *American Indians*[1] seem to have developed from groups that entered the New World from Asia, coming across Bering Strait in successive waves over a very long period of time. The earliest migrations, according to most authorities, could not have occurred before the end of the last glacial stage (Wisconsin), some 15,000 to 20,000 years ago,[2] but they probably began soon after the recession of the ice sheets, and are known to have continued until well into the Christian Era.

The peoples that inhabited America prior to its discovery by Europeans differed very greatly among themselves in physical characteristics as well as in language and culture. Some of the American groups, such as certain of the Indians of the northwest coast of North America, with their round heads, low-vaulted skulls, and flattish faces, are actually closer in all physical features to Asiatic Mongoloid groups than they are to the tall, long-headed Indians, with high-vaulted skulls and straight noses, that inhabited the eastern woodlands. Thus, instead of forming a single well-defined "Red" race, as used to be thought, the American populations are instead a racial complex that must be classified as a part of the great "Mongoloid" yellow-brown group of peoples.

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[1] The authors are indebted to Dr. Georg Neumann, of the Department of Zoology, Indiana University, for assistance in preparing the account of the American Indians, as well as for valuable suggestions and criticisms in connection with the remainder of this chapter.

[2] Discovery of the very ancient Folsom culture in the Southwest in unquestionable association with an extinct Pleistocene species of bison, the finding of artifacts in the uptilted early post-glacial lake beaches along Lake Huron, and the presence of human remains and artifacts in Florida in strata containing the bones of various species of extinct mammals shows that man was widespread in North America very soon after the close of the Wisconsin glacial epoch, and has led some students recently to postulate a somewhat earlier time of entry than has hitherto been considered possible.

Both the Asiatic and the American series within this Mongoloid complex comprise more recent round-headed elements, superimposed on an earlier long-headed population that was probably derived from the original undifferentiated White-Mongoloid stem, or possibly, according to Hooton, from "White" (proto-Mediterranean?) stock. Some of the Asiatic yellow-browns contain a considerable Negroid element that is apparently absent from the American populations. Both the Asiatic and American Mongoloid groups share a yellow to brown skin, coarse black hair that is usually straight but occasionally wavy, and a characteristic prominence of the cheek-bones.

Three basic racial types can be recognized among the American Indians, two of which may be further subdivided. The first is a very ancient, long-headed assemblage, which may be grouped as the *Paleo-Amerinds;* the second is a more recent round-headed group, the *Neo-Amerinds;* and the third consists of the very distinctive far-northern peoples called the *Eskimo.*

The *Paleo-Amerinds* evidently form the oldest element in the populations of both North and South America, whether judged by stratigraphic records, by their more primitive physical characteristics, or by their geographic distribution. This complex of long-headed groups, at the time of the discovery of America, occurred in relatively pure form chiefly in marginal and "refuge" areas in the two continents. The long-heads were the first migrants into the New World, and seem to have come to occupy most parts of both continents. In North America two divisions of these Paleo-Amerind peoples are recognized by some authorities—the *Southwestern Longheads* and the *Eastern Longheads* or Eastern Woodland Indians.[1] The two groups are admittedly hard to distinguish, and their interpretation presents a number of difficulties, especially with reference to the homogeneity of the former, and whether they represent successive migrations or differentiated from a single original long-headed stock after its entry into America.

In general, the *Southwestern Longheads* have a skull with low or medium-height vault, a low and somewhat broad nose, hair that is sometimes wavy, and a face that in some groups was long and narrow. However, they show a considerable amount of regional differentiation in such features as height of skull vault and facial proportion (some having quite short faces), and some groups had a notably small skull. Once doubtless very widespread, this group has left traces of its former presence in eastern North America (Kentucky), and also included among its members the preagricultural *Basket-Makers* of the Southwest. Today it is represented chiefly in northwestern Mexico, southern California, and especially in Baja California, and occurs as disjunct relicts in the highlands of Central America. It also survives in admixture with Earlier Roundhead stocks in some of the Pueblo tribes of the southwestern states. Men of this type are the chief and perhaps the only ones represented in the first and oldest of the recognized archeological horizons of North America—the preagricultural stage of hunting cultures, in which the use of pottery was unknown.

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[1] These and the groups subsequently discussed are known under various names. In the terminology of von Eickstedt (*Rassenkunde und Rassengeschichte der Menschheit*, Stuttgart, 1934) the equivalents of the names here used are as follows: North America: Southwestern Longheads = Margids, Eastern Longheads = Sylvids, Earlier Roundheads = Centralids, Later Roundheads = Pacifids, Plains Indians = Prairids (Neumann), Eskimo = Eskimids; South America: Lagoa Santa race = Lagids, Amazonian Longheads = Brazilids, Pampean Roundheads = Pampids, Andean Roundheads = Andids.

The *Eastern Longheads* have long, high-vaulted skulls and relatively narrow faces, with fairly high, somewhat narrow, straight noses. They are typified by men of the Algonquian- and Iroquois-speaking tribes that inhabited the eastern forested parts of North America, many of whom could pass for dark-skinned European types. Although concentrated in the eastern woodland regions at the time of the coming of the Whites, they seem once to have had a much wider distribution which extended even to the Pacific Coast. With the advent of the Earlier Roundheads, the Eastern Longheads were displaced from much of their original territory; but they survived both as relatively homogeneous populations in the northeastern and eastern marginal areas, and as minor elements in the later populations of the southeastern states and the prairie regions. Paleo-Amerinds, in large part doubtless of Eastern Longhead type, were responsible for the cultures of the second archeological horizon throughout eastern North America—the horizon in which the first pottery (fiber and granular tempered) made its appearance, and which is tentatively dated as extending from 900 to 1100 A.D.

Long after the coming of the Paleo-Amerinds to America, there began a series of migrations of round-headed, more Mongoloid peoples who gave rise to the *Neo-Amerind* populations of the New World. An earlier period of invasion, of unknown date but possibly between 5000 and 10,000 years ago, brought in men of a physical type which we may call the *Earlier Roundheads*. A second and much more recent series of migrations seems to have continued until well after the beginning of the Christian Era, the peoples of this wave being of still more Mongoloid type—the *Later Roundheads*.

The *Earlier Roundheads* have round, high-vaulted skulls, and faces that are somewhat broader than those of the Paleo-Amerind longheads. They poured down the western side of North America, sending offshoots eastward into the central and southeastern parts of the continent, and eventually pushing southward to occupy much of Central and western South America. In the eastern United States the forerunners of this round-headed group first began to appear toward the close of the period represented by the second archeological horizon. They became more numerous in this area during the third (early agricultural) period, tentatively dated as between 1100 and 1400 A.D., and subsequently replaced the original long-headed Paleo-Amerind population throughout the entire region of the southern states except the Carolinas and Virginia. All along the zones of contact, intermingling took place between the older stock and the invaders, producing mixed groups and more or less hybrid cultures. The Upper Republican culture of Nebraska, and one of the later cultures of southern Ohio, were the product of such mixed peoples. (The majority of the famous Ohio mounds, however, were built by earlier Hopewellian people of nearly pure Eastern Longhead stock.) The Mayan civilization of Guatemala, Honduras, and Yucatan, and the advanced Peruvian culture, were the product of pure or mixed peoples in which the Earlier Roundhead stock or its descendants predominated. The great Toltec and Aztec cultures of the Mexican Plateau were developed by Indians of mixed Southwestern-Longhead and Early-Roundhead ancestry.

The *Later Roundheads* came into North America by way of the northwestern portal at a comparatively recent date. They have round heads, low-vaulted skulls, with a rather flat cranial base, and large, relatively flat faces. The Aleuts and some of the Indians of the northwest Pacific coast are good examples of this physical type. The peoples of this stock spread over much of the western part of North America, but never reached the eastern parts of the continent, nor into Central or South America. At the time of the discovery of America they occurred chiefly in two regions. In the north they occupied a large area of continuous distribution, from Alaska eastward to the shores of Hudson Bay and south along the Pacific Coast and in the Cordillera to Washington and Oregon. Thence southward they were represented only by scattered groups in central California and by mixed populations in the Central Rockies and Great Basin, until a second large and relatively unmixed group was encountered in western Texas, New Mexico, southern Colorado, and northern Chihuahua and Coahuila. They are known to have reached this southwestern area about 1300 A.D. The Later Roundhead stock, in pure form (for example, the Apache) or in mixtures with older groups (for example, the Navajo), constitutes the basis of much of the non-Pueblo Indian population of the Southwest.

The *Indians of the Plains* show a rather wide variety of physical types. In the Northern Plains and Prairie regions many of the tribes are of nearly pure Later-Roundhead type. A minority exhibit almost unmixed Eastern-Longhead features, and a considerable number have evidently arisen as the result of hybridization between Later Roundheads and Eastern Longheads. As among Indians elsewhere on the continent, there is no close correlation between language and culture, on the one hand, and physical type on the other. The Crow Indians are an excellent example of the Northern Plains hybrid stocks, and the Indian head on the Buffalo nickel shows a type common in this area, with a long but low-vaulted skull, a face that is heavy, relatively large and somewhat flat, and a prominent, often aquiline nose. The Indians of the Southern Plains and Prairies are of different aspect. They have arisen largely through the intermingling of Earlier and Later Roundheads, producing types with similarly heavy faces, but brachycephalic, broader-nosed, and often with a relatively high cranial vault.

The remaining North American group of Indians is the *Eskimo*, found along the Arctic Coast from Alaska to Greenland. This far northern people, though clearly Mongoloid, shows the greatest amount of differentiation of any of the American Indians, and constitutes a very distinctive racial type. The skull is very long, the face is disharmonic, with narrow forehead and unusually prominent cheekbones, and the nose is narrow. The Eskimo probably entered North America at a relatively recent date, although almost certainly before the main migration of the Later Roundheads.

The Indians of South America have been much less thoroughly studied than those of the northern continent, but in general they exhibit a similar distributional pattern. One can recognize an older long-headed type, the *Lagoa Santa race*, which appears to be a counterpart of the Southwestern Longheads; an apparently more recent *Amazonian-Longhead* type, which perhaps corresponds to the Eastern-Longhead stock of North America; and a considerably more recent group of round-headed *Neo-Amerinds*, all of whom belong to or have developed from the same basic stock as the Earlier Roundheads of the north. The Lagoa Santa race is at present concentrated in the "refuge" area of the eastern Brazilian highlands, with isolated remnants in pure or mixed form in the Guiana and Colombian highlands, the Andean region, and southward to Patagonia. The Amazonian Longheads inhabit the great Amazon Basin west to the mountains and south to the Chaco. They also occupy the coastal regions of Brazil, as well as the Guianas and the Antilles, and are represented by minor relict elements in Panama, Colombia, and Venezuela. Throughout western South America and in the greater part of the southern plains regions, the original long-headed populations have been replaced by round-headed Neo-Amerinds. The parent stock of Early Roundheads seems still to be represented in the extreme northwestern part of the continent, but southward its descendants have differentiated into two types—the *Pampean Roundheads* of the Chaco and Argentinian Pampas, and the *Andean Roundheads* of the coastal and mountainous regions of Peru and Chile. It was peoples of this latter group that had developed the very advanced Peruvian culture encountered by the Spanish conquerors of South America.

CHAPTER XXXIV

The Mechanism of Evolution

An Evaluation of Some Evolutionary Processes

THE preceding chapters have presented many of the data that attest the reality of evolution as a historic process; today there can be no serious scientific doubt that organic evolution has been and is a universal biological principle or that all living organisms owe their present form and function to its long-continued operation. But there is a very marked difference between the biologist's certainty of the fact and of much of the course of evolution, and his ability to analyze, describe, and evaluate the precise biological processes that bring it about.

It is interesting, and even paradoxical, to recall that the original acceptance of evolution as a biological principle was due to Charles Darwin, who, with his followers, established the fact of evolution largely as a background for a proposed explanation of the factors that account for it. The early Darwinians, however, were more impressed with the necessity of proving the fact of evolution than with critically examining the mechanisms that were supposed to bring it about; and once the fact was felt to be well established, they were chiefly interested in reinterpreting the facts of biology in the light of evolution and in working out the evolutionary histories and relationships of various groups of animals and plants. This was no doubt partly because the early opposition to Darwin was a denial of the reality of evolution and partly because the methods of comparative morphology, paleontology, and comparative embryology, then at the forefront of biology, tended to emphasize the broad outlines of evolutionary history rather than to encourage experimental studies of its details.

A brief account of Darwin's theory of evolution through natural selection has been given on pages 300 to 303. Proposed in 1859, Darwin's postulates have undergone many changes and emendations in 80 years of increasing biological knowledge. It will be noted to what a large extent he utilized the concepts of inheritance and variation, although it was not until after 1900 that biology began to acquire an exact definition and knowledge of these fundamental processes. Today it is evident that many, perhaps most, of the clues to the mechanism of evolution are to be sought for in the field of genetics. Certainly there is much reason to believe that the mutations and chromosomal changes, which have been demonstrated—if not explained—by controlled experiments, provide an adequate fund of inherited variations to meet the logical requirements for evolution. There is still some question as to whether known types of mutations exhibit all the qualities that are found in specific differences, but in view of the demonstrated ability of mutations to show combining and additive effects in inheritance, even this question seems to be obtaining an affirmative answer. Thus, although many of the types of variation that Darwin cited as acted upon by selection have proved to be noninheritable, a sufficient supply of heritable variations has been demonstrated to meet all the needs of Darwin's theory.

The biologist's concept of inheritance has also been greatly changed since Darwin's time, but it is difficult to see how any of the functions that Darwin visualized for his rather vague concept of "blended inheritance" are not abundantly fulfilled by the many intricate but well-known patterns of Mendelian inheritance. Indeed, when one considers modern findings on the varied and often seemingly unrelated roles of a single gene, the interrelations of modifying and multiple genes, and the ability of recessive mutants to persist—unexpressed and unchanged—in the phenotype for many generations, heredity appears to be a much more potent and versatile factor for evolutionary processes than Darwin conceived it.

It is perhaps in natural selection itself that modern ideas of evolutionary processes show the greatest change in and expansion of Darwin's original concepts. Most of his actual data concerning selection were obtained by his study of the methods of the practical breeder, and he was greatly impressed with the efficacy of long-continued selection in improving and differentiating domestic races of animals and plants. As a consequence he seems to have conceived of selection as chiefly a direct process, operating to discriminate among individuals and to favor markedly superior individuals at the expense of the majority of the population. Today, thanks to the detailed experimental data from genetics, the biologist has a somewhat different estimate of both the power and limitations of selection. Without doubt, nature does exercise selection among individuals, but here selection appears to operate more as a check on definitely disadvantageous phenotypes than as a direct means of preserving for reproduction the most favorable genotypic constitutions. In other words, although definitely disadvantageous mutations tend to be eliminated to the extent that they attain phenotypic expression, there is little reason to believe that selection within a population of interbreeding individuals can often effectively favor any single advantageous mutation, or even eliminate unfavorable genes until they have appeared in the soma.

On the other hand, a potent—though somewhat different—effect of natural selection is now seen in its ability to discriminate among groups and races of related individuals after they have already differentiated into more or less separate breeding populations. Here differences in the fertility, viability, and adaptive fitness of competing groups provide both theoretically favorable conditions for and biologically demonstrable cases of natural selection. Thus the most important role of natural selection has been to a large extent relegated to a somewhat later stage of the evolutionary process than Darwin conceived it.

The initial changes within a population appear to be more frequently due to the repeated occurrence of mutations (and their combining effects), and the various types of isolation that segregate certain mutations within small interbreeding groups of the original population. This appeal to isolation as an evolutionary factor is not so much the product of logical necessity as it is the result of discovery, from a wide variety of experimental and observational studies, that small effective breeding populations are the rule rather than the exception among the great majority of organisms. Barriers to wide interbreeding are of many sorts. The most obvious, and hence the first known and studied, are the various types of geographic barriers that come to break once continuous populations into spacially separated portions; but other types of barriers not so obvious are equally effective and perhaps far more common. Among these are ecological differences in habitat or breeding season that tend to keep one group of individuals from actually encountering another, and the many kinds of psychical, anatomical, or physiological differences that either inhibit mating or prevent the production of fertile offspring. Perhaps the development of such a psychical, anatomical, or physiological difference within a formerly interbreeding population may require at least a temporary interval of spacial or ecological isolation for its development; but our present knowledge of the movements and dispersals of natural populations indicates that periods of spacial isolation are of relatively frequent occurrence.

Given mutations as the basis for changes in the characteristics of any group of organisms, and a sufficient isolation of small interbreeding stocks, differences within the formerly homogeneous population will and do result. Natural selection may hasten or delay this differentiation, depending, in part, on the kind of mutations that occur and on the nature of the habitat occupied by the stock in which a given mutation[1] took place. Once differentiation has taken place, natural selection will often further discriminate between the different stocks, according to their adaptations for occupancy of any common habitat that they may invade. This much seems amply demonstrated by present-day studies of actual populations of both wild and "laboratory" races of animals and plants. Moreover, the careful scrutiny of many other species and races of wild organisms has brought to light a multitude of spacial, ecological, and genetic relationships that bear witness to the interplay of mutation, inheritance, isolation, and differential selection in developing the qualities that characterize them and that distinguish them from other closely related species and races. Such evidence is clearest where we are concerned with differences among species, or among the subspecies or races and the even smaller, isolated, intraspecific populations that show differentiation. Here the biologist is dealing with evolutionary processes still in operation, the steps being small enough to be followed and much of the evidence still extant. Whether the differences between genera, families, and larger taxonomic groups of organisms are comparable with those that exist between and within species is perhaps still a question for debate, although it seems rather difficult to point to any essential unlikeness in kind or degree that cannot be accounted for by the immensely longer time that intergeneric and interfamilial differences have had to accumulate, and by the loss of much of the pertinent data.

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[1] For instance, color mutations in the field mouse Peromyscus are comparatively frequent. There is much field and experimental evidence that mutation toward a lighter coat color is advantageous for a stock that occupies light-colored soils and

We have here attempted briefly to summarize a rather widely held modern evaluation of evolutionary processes which is still essentially Darwinian, in spite of considerable modifications that have to be made in many details and definitions. But Darwin was not the only biologist who advanced theories to account for evolution. In fact, Darwin himself did not believe that natural selection and its several subsidiary theories would account for all evolution and he definitely accepted several of the factors that had previously been advanced by Lamarck. Today, most of the older alternative theories of evolution have been either disproved or abandoned as essentially outside the scope and province of biology; but many of them were long incorporated in evolutionary studies and have had a marked influence on much biological thought.

Other Evolutionary Theories. Prior to Darwin's time, a French biologist, Lamarck, presented an evolutionary theory that had many attractive features. This theory, known today as *Lamarckianism*, was based upon the concept that the effects of use and disuse of organs were inherited and that adaptation to environment resulted. Unfortunately for this hypothesis, the effects of use and disuse are restricted to the

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definitely disadvantageous for mice that occupy dark soils; just the reverse is true for mutations toward a darker coat color, but either type of mutation appears equally likely in either situation.

somatic tissues, and genetics has never afforded the slightest support for the idea that the soma plays any part in heredity. Most biologists today are unwilling to concede that the Lamarckian hypothesis has any validity; but there remain a few, especially among the ranks of the paleontologists, who still hold that no other theory can account for such phenomena as the continued dwindling and final disappearance of vestigial organs or the gradual improvement of the mechanical arrangements in bones, joints, muscles, and tendons.

Another theory that has had considerable vogue among paleontologists and some students of evolution, but that seems impossible to test, is that of *orthogenesis.* This is the idea that particular groups of organisms possess an inherent tendency for continued change in a definite direction. The proponents of this hypothesis point to the fact that the paleontological record shows many groups of organisms apparently starting along some particular path of evolutionary modification and continuing to change in this direction far past any obvious need—indeed, sometimes to such a point that the very existence of the group is imperiled. Thus the branched horns of the deer group culminated in the tremendous antlers of the extinct Irish deer, in which they attained a spread of 11 feet and would appear to have been actually disadvantageous. In order to explain the origin of characters as inconspicuous rudiments in the early development of a group and their subsequent steady development to great heights of specialization and even of apparent overspecialization leading to extinction, the theory of orthogenesis was proposed.

This theory is not really an explanation of evolutionary change, since it makes no attempt to analyze the nature of the mysterious "internal tendency to change in a definite direction." Furthermore, many of the supposed instances of orthogenetic change are now known to be the direct result of a differential growth rate of different parts of the body; as size of a species increases and the duration of growth is prolonged, the faster growing organs may attain undue size or become developed in other ways out of proportion to the rest of the body, leading to the condition formerly attributed to "overspecialization." On the whole, therefore, there are no present grounds for accepting orthogenesis as a valid evolutionary hypothesis.

PART IV

THE ECONOMIC AND SOCIAL INTERRELATIONSHIPS OF ORGANISMS

CHAPTER XXXV

The Physical Environment of Organisms

We have seen something of the evidence that all organisms share a common kinship based upon descent from a common ancestry far back in geologic time. In this kinship, we have the clue to the essential similarity of protoplasmic composition and cell structure throughout the living world, as well as to the more detailed resemblances that are shown by organisms with a less remote common ancestor.

There is another sense in which all forms of life are related. This relationship consists in the intricately interwoven dependencies, competitions, and exploitations that exist among all forms of life through their necessity of maintaining themselves by the capture and expenditure of energy. Here the relationship is primarily an *economic* one, far too complex to be known in full detail, yet clear enough in at least two respects to be undoubtable. Part of our knowledge of this relationship comes from a consideration of the "energy cycle," in which we can trace the maintenance of all life to the utilization of energy that is ultimately derived from the sun; another part comes from the incomplete but considerable portion of the economic and social interplay among organisms that biologists have been able to trace and, to some extent, to measure.

THE ENERGY CYCLE IN THE ORGANIC WORLD

All being alive involves a constant expenditure of energy, and, precisely as in any engine, a part of this energy is never again available for any life processes. With no significant exception, all this energy upon which life depends comes from the sun; and until it is finally dissipated beyond the use of any protoplasmic device, it goes through a series of transformations and interchanges that support the entire organic world. In the sense that the energy from the sun is gradually lost and must be continuously replaced, the process is noncyclic; but in its turnover and re-utilization of raw materials and in the often long series of transferences of energy from one organism to another—always with some loss of total usable energy—a cyclic relationship is well marked.

The Original Capture of Energy. Roughly, about one-millionth of the sun's constant output of energy falls upon the earth in the form of radiation, and this condition has existed since the origin of the earth. Of this energy, some 0.3 to 3 per cent is conserved and utilized in the building up of protoplasm and the maintenance of life. The ability to capture and transform this energy is confined to the green plants and is due to the peculiar properties of chlorophyll, which is able to transform light energy into chemical energy and store it in the form of chemical compounds.

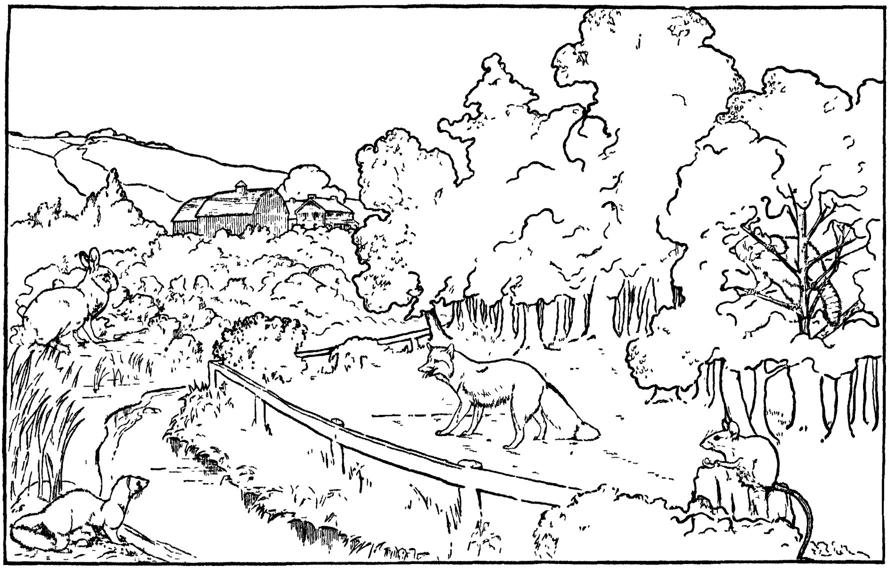

FIG. 143. *All living things—plants, animals, and man—are bound together in an intricate web of social and economic interrelationships.* (*Modified from Cornell Rural Leaflet.*)

The Raw Materials Involved. Protoplasm and cell products are composed chiefly of carbon, oxygen, hydrogen, and nitrogen, together with smaller quantities of calcium, phosphorus, sodium, potassium, sulphur, magnesium, iodine, copper, iron, zinc, and a few other elements. These are distributed more or less generally over the earth, either as elements or as simple compounds, and, as such, contain no energy that is available to living organisms.

The Storage of Energy; Food Synthesis. The building of organic molecules out of the simpler inorganic molecules and elements requires an expenditure of energy. Once synthesized, the complex organic molecules contain not only the original raw materials (atoms and simple combinations of atoms) but also the energy that was necessary for their construction. We have seen (in an earlier part of the book) that the complex molecules from which protoplasm is built include proteins (or their component amino acids), carbohydrates, and fats, and that these same substances are the foods on which organisms depend for growth and all catabolic processes. Only plants have the ability to synthesize these substances from simple inorganic material, and only the green plants can perform the basic photosynthesis in which light is captured and stored as chemical energy. Once this synthesis has taken place and sugar is available, other plant tissues can utilize the energy in the sugar (or its derivatives) by oxidation, to build simple nitrogen compounds into amino acids and proteins and simple carbohydrates into fats.

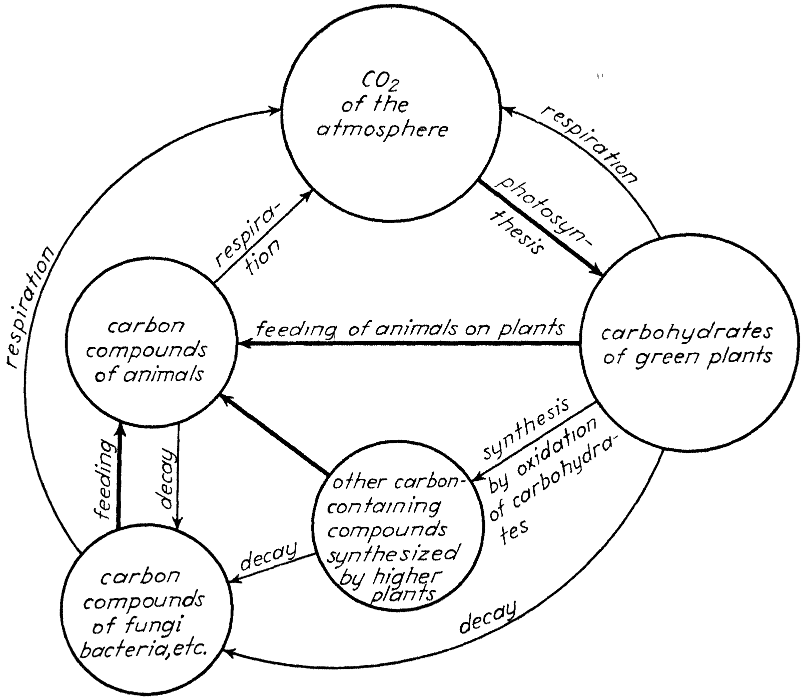
CO_2 of the atmosphere
respiration
photosynthesis
respiration
respiration
carbon compounds of animals
feeding of animals on plants
carbohydrates of green plants
synthesis by oxidation of carbohydrates
feeding
decay
other carbon-containing compounds synthesized by higher plants
decay
carbon compounds of fungi bacteria, etc.
decay

FIG. 144.—*Diagram of the carbon cycle in the organic world.*

The green plant takes in carbon in the form of carbon dioxide from the air (through its stomata) or in solution in water, and takes in water from the soil (through its root hairs and vascular system). Carbon dioxide and water are combined by photosynthesis to form sugar, with the giving off of oxygen as a by-product. Nitrogen is obtained in the form of ammonia or nitrate salts, in solution in the soil water, as are the necessary supplies of calcium, phosphorus, potassium, sulphur, etc. From these raw materials are synthesized all the food substances needed for building more protoplasm (growth and reproduction), for expenditure in maintaining life, and for storage against future needs. The energy of the sun is thus stored or bottled, so to speak, in the form of the complex molecules of protoplasm and plant products. Altogether, this amounts to billions of tons of synthesized carbon compounds in existence on the earth.

The Release of Stored Energy. Free oxygen is not a necessity in any of these building-up processes and is, in fact, a waste or by-product of photosynthesis; but it is required for the utilization of the energy stored in food. All utilization of this energy is by means of oxidation, and oxygen is thus the key that unlocks the stored energy for use. As a consequence, all living things require a supply of oxygen and, except for some bacteria and a few fungi, algae, and parasitic animals, are dependent upon uncombined oxygen, which they acquire by respiration.

The Transference of Stored Energy. Once the plant has built up the higher carbon and nitrogen compounds, all other forms of life crowd in to share the product. Colorless plants, unable to utilize the sunlight, and animals, unable to synthesize any basic food substance, must exist upon what they can secure directly or indirectly from the green plants. Many elaborate "food chains" have been developed, in some of which the last and most powerful animal, or the last and most remote parasite, obtains its food at fourth, fifth, sixth, or seventh hand after its original synthesis by the plant. The synthesized molecules may circulate so long as they never are broken below the level of simple sugars or amino acids, but in each organism and at each transference, some of them must be broken below this level to provide animal and plant energy.

Moreover, not all protoplasm is eaten. Many plants and animals die and fall to the ground, where their dead substance would accumulate and remain locked up were it not for the processes of *decay* carried on by special soil bacteria. In these processes, the organic substances are broken down with loss of heat to the soil and atmosphere, and the original elements and inorganic compounds are returned to the air and soil, where they again become available for the carbon and nitrogen cycles. A similar return is also constantly made by the respiration and the nitrogen catabolism of all living organisms.

The *soil* thus plays a very important part in the energy cycle. It not only maintains a huge population of bacteria, fungi, and other organisms that slowly but constantly oxidize the compounds that have escaped the catabolism of higher organisms, but it also serves as a storehouse for the end products of this decay until they are again taken up by the green plants to enter the synthesis part of the cycle. In fact, a very considerable part of the soil is formed by the decay-producing organisms themselves and the end products of their oxidative processes.

SOME QUANTITATIVE CONSIDERATIONS

The preceding account of the energy cycle has been given largely in qualitative terms. Actually, the whole process is capable of being treated in a quantitative way. The utilization of the radiant energy from the sun to propel all life processes is governed by the same quantitative energy laws that hold for any engine or any physical utilization of power, and the same total energy is freed whether foods are burned under a boiler or oxidized in the animal or plant body. As in the engine, only a part of the energy released by oxidation within the organism is convertible into useful work, and part is lost as heat. In human muscle, the efficiency of the conversion, some 20 to 33 per cent of the total energy available for work, compares favorably with that of the best existing steam engines.

SOME QUANTITATIVE VALUES

1 gram of sugar	by oxidation yields	4.1 Calories
1 gram of fat	by oxidation yields	9.4 Calories
1 gram of protein	by oxidation yields	5.6 Calories
1 gram of carbon	by oxidation yields	8.0 Calories
1 gram of hydrogen	by oxidation yields	34.5 Calories

One Calorie is the quantity of heat necessary to raise the temperature of 1 kilogram of water 1°C.[1]

One pound of bread will give approximately 1,200 Calories.

Man needs 1,500 to 5,000 Calories per day.

One acre produces from 1 to 4 tons of carbohydrates per year.

One square meter of green-leaf surface synthesizes 1 to 2 grams of sugar per hour.

Bread contains 53.3 per cent carbohydrate, 9.1 per cent protein, 1.6 per cent fat, 35.0 per cent water (from which no energy is obtainable).

THE PHYSICAL ENVIRONMENTS IN WHICH ORGANISMS LIVE

In considering the various kinds of interrelationships that bind all the organic world into a huge economic and social complex, it is necessary to see something of the problems and needs imposed upon these organisms by the conditions of the physical world in which they live. For purposes of analysis, we may subdivide the physical environment into the influences of the *medium* in which the organisms live, and the *physical* (and *chemical*) *factors* that condition the medium and determine the reactions and metabolic processes of the organisms within it.

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[1] More exactly, the amount of heat required to raise one kilogram of water at 15°C. to 16°C.

The Media in Which Organisms Live

All life of which we have any knowledge is confined to a shallow zone at the surface of our earth, where *soil*, *water*, and *air* meet and intermingle to a slight depth. Thus any organism must live in water or air or soil or in some combination of the three. These three media differ markedly in many physical properties, and each presents its own special problems to the organisms that live within it. The different requirements for mechanical support and the different problems of locomotion, adjustment to temperature changes, respiration, food gathering, and reproduction that are conditioned by aquatic, aerial, and terrestrial media are so unlike that they impose many structural adaptions upon organisms and enable us ordinarily to know from a morphological inspection whether a given organism is fitted for life in water, on the land, in the soil, or for border-line or alternate existence in two (or more) of these media.

The Medium and Mechanical Support. Because of the great buoying power of water, aquatic organisms can attain much greater size and weight and a much greater expanse of surface with a given amount of skeletal or supporting tissue than can land animals. This buoyancy of water is utilized in two quite different ways. On the one hand, it has permitted the skeletonless development of such large marine organisms as the jelly fish and the octopus among animals and the giant kelps and other huge algae among the plants, and on the other, it has permitted the development of heavy armor and protective coverings, as in the starfishes and shelled mollusks, without the necessity for powerful locomotor organs. On land, the common earthworm and slug represent something like the upper limits in size for a skeletonless, motile organism; in the sea, animals with as little or with less mechanical support may attain a weight of a ton or more.

The Medium and Locomotion. Differences in the problems of locomotion in water, on land, and in air are even more marked than those of mechanical support. The motile, aquatic animal has something of the same problems as the lighter-than-air dirigible. Although not lighter than the water (or very little lighter), its weight is supported by the medium, and its locomotor organs have only to propel it through the water. Since, however, water is a comparatively dense medium, movement through it meets with great resistance unless the force required to displace the water is very largely balanced by the push gained when the water, in turn, displaces the moving object. As a consequence, "streamlining" is highly important; and all motile aquatic organisms, except those that simply drift and a few slow crawlers over the bottom, are distinguished by some type of streamlined form. In terrestrial animals, on the other hand, locomotion involves not only propulsion but the support of the body in a medium that supports less than one-thirtieth of the body weight. All locomotor movements must involve either the overcoming of a relatively great friction with the earth (and this becomes increasingly difficult with each increment of size and weight) or the lifting of the body and the maintaining of its equilibrium as it is moved forward. As a consequence, all the larger and more motile terrestrial animals have the greater part of the body weight accounted for in *supporting and locomotor appendages*. Here streamlining is generally less important, although it becomes a factor in the adaptation of certain terrestrial animals to high rates of speed. Flight through the air demands still other highly specialized adaptations, notably the development of great skeletal rigidity with light weight, streamlining, the acquisition of powerful flight muscles, and skeletal modifications for their efficient origin and insertion.

The Medium and Fluctuations in Temperature. The temperature relationships of water differ markedly from those of air or land. The most important of these differences are due to the specific heat of water and its latent heats of freezing and of evaporation. By the *specific heat* of water is meant the amount of heat (calories) required to raise 1 gram 1°C. We have already seen that this is 1 calorie,[1] and water, with a specific heat of 1.0, may be compared with some other substances; lead, 0.012; mercury, 0.0334; carbon, 0.16; sand, 0.15; alcohol, 0.535. Only ammonia exceeds water in specific heat, and nearly all other substances have a markedly smaller value than water.

By *latent heat* is meant the amount of heat required to change water from its solid state to a fluid state and from a fluid state to a gaseous state without a change in temperature. To change 1 gram of ice to water (with the temperature kept at 0°C.) requires 80 calories, and when 1 gram of water freezes, it gives up 80 calories to the surrounding medium. The latent heat of evaporation is even greater. To change 1 gram of water to 1 gram of water vapor without a change of temperature requires from 590 to 540 calories (depending upon the temperature), and this amount of heat is given up when the water vapor condenses. In this respect, water is hardly approached by any other substance.

As a consequence of these properties, the temperatures of bodies of water tend to be very stable and to change relatively slowly. In a 24-hour period, within which our local air and soil surface temperatures not infrequently change as much as 30°C., our local ponds and streams will show very small changes in temperature, hardly more than 5° at most, and in the course of a year will vary hardly more than 15 or 20°.

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[1] One-thousandth of a great Calorie.

The Medium and Respiration. All organisms, irrespective of the medium in which they live, must be able to secure oxygen and excrete carbon dioxide. Except for a few protozoa, a few algae, and a number of bacteria, which are able to obtain combined oxygen from various of its compounds, all organisms, to meet this need, depend upon a gaseous interchange with the medium that surrounds them.

For terrestrial animals living in an atmosphere that is one-fifth oxygen and much less than 1 per cent carbon dioxide, the chief problems of respiration are to provide a sufficiently extensive respiratory surface to meet needs of gaseous interchange and to protect such a surface from too great a water loss. (All membranes permeable to oxygen and carbon dioxide are also freely permeable to water vapor.) A number of small terrestrial animals solve this problem by utilizing the body surface for respiration and avoid desiccation by remaining within permanently damp situations; but a much more successful and less restricted terrestrial existence has been achieved by the development of special, *internal* respiratory surfaces that are thus protected from evaporation and must be aerated by special breathing movements. Such structures are the lungs of the vertebrates, the tracheae of insects, and the modified internal gills of arachnids (book lungs) and of terrestrial mollusks.

For aquatic organisms, the interchange is between the gases of the tissues and the gases dissolved in the water. Since there is no evaporation problem and since mechanical support by the water permits a comparatively large development of surface area, the utilization of the body surface is much more practicable for aquatic than for terrestrial organisms. But even among aquatic organisms, there are a number of factors that limit the usefulness of the body surface for respiration. Increasing size or metabolic rate may finally make the surface area of the body inadequate for a sufficient gaseous exchange; motile or burrowing habits may require an integument too thick and tough to serve as a respiratory membrane; and the necessity for streamlining limits the amount of surface area that can be utilized for respiration. Under these conditions, the aquatic organism has to provide some special respiratory device, nearly always areas of thin tissue through which rapid gaseous interchange can be carried on between the body fluids and the water. These aquatic respiratory organs, *gills*, are of many types, but in fast-swimming or bottom-dwelling forms, they are usually enclosed in some protected chamber and aerated by special breathing movements.

Among the plants, a somewhat comparable contrast between adaptations for terrestrial and aquatic life occurs. The necessity for respiration under desiccating conditions is met, in terrestrial plants of dry situations, by a water- and respiration-proof *cuticle* and the development of *stomata,* which permit respiration and yet prevent undue water loss. In normally submerged plants the cuticle and stomata are absent, but in many amphibious plants that are often partially submerged beneath oxygenless water, special air ducts are developed to carry atmospheric air to the submerged parts.

The Medium and Food Manufacture in Plants. The problems of obtaining the raw materials and energy for food manufacture are not greatly different for terrestrial and aquatic plants. The penetration of light into the water permits some photosynthesis to a depth of perhaps 100 meters or more, although the great majority of aquatic green plants are confined to the upper 10 to 20 meters. Carbon dioxide is present in solution in nearly all natural waters and is constantly being supplied by the respiration of living aquatic organisms and the decay of dead ones. The other requisites for food manufacture are also in solution and are available by diffusion through the permeable surface membranes of aquatic plants.

The Medium and Food Capture by Animals. Both terrestrial and aquatic animals show a wide variety in the kinds of foods they seek and in the methods employed to secure it. Aside from the associated problems of locomotion, one of the main differences between the water and the land is the relatively huge amount of food material that is more or less generally dispersed in the upper layers of nearly all aquatic situations. This food is chiefly in the form of small to minute living plants and animals, together with a considerable quantity of nonliving food—dead organisms or fragments of them. This abundant and constant food supply has resulted in the development of an important aquatic fauna that feeds upon it. The members of the fauna include:

Motile Food Strainers. Among these are many fishes, some of the whales, and a number of both small and medium-sized invertebrates. All are equipped with some type of *sieve* (frayed whalebone, gill rakers, or mouth or foot bristles), through which quantities of water are strained while the animals swim through the suspended food particles. These animals do not pursue individual prey but simply strain a sufficient quantity of water to yield the requisite food.

Nonmotile Food Strainers of Quiet Waters. These are sedentary forms, such as the sponges, oysters, clams, and others, that by means of cilia or flagella cause a slow, steady stream of water to flow through body passages that are equipped to retain the food particles carried in with the water current. Most of these organisms utilize the same water currents to bathe their respiratory surfaces and so combine breathing with food gathering.

Nonmotile Food Strainers of Flowing Waters. This is a smaller group but is very characteristic of riffles and gentler rapids in small and large streams. It is largely composed of aquatic insect larvae that either spin silken nets or, clinging to some stable support, hold sievelike body parts (bristly fringed forelegs or mouth parts) out into the current and wait for food particles that are brought to them.

Food Trappers or Stingers. The most conspicuous of these are the jellyfishes and other coelenterates, which, floating near the surface, trail tentacles armed with stinging cells through the densely populated subsurface waters and rely on chance to bring their food organisms into contact with the triggers that discharge poisoned stings. For the smaller jellyfishes, the food organisms are members of the great floating assemblage of rapidly reproducing minute animals; for the larger coelenterates, it is likely to be some of the host of smaller motile food strainers that feed in the subsurface waters.

Most of these aquatic schemes of food capture have counterparts among terrestrial and aerial animals, but proportionately they are far more important and support a far larger fauna than on land, where the pursuit and capture of individual prey is more generally the rule.

The Medium and Reproduction. We have already seen that external fertilization is essentially an aquatic adaptation and that all self-motile gametes are swimmers. We have also seen—in the vertebrates, at least—that the original oviparous habit involved water as a medium to protect the eggs from shock or dessication.

Terrestrial life has either necessitated a return to the water for reproduction, the dependence upon permanent or recurrent water films in the terrestrial habitat (zygote formation in the mosses and ferns), or the development of special terrestrial adaptations. Among animals, these have been chiefly the habit of internal fertilization and the development of either shelled eggs or a viviparous habit. In addition, the terrestrial vertebrates have acquired special extraembryonic membranes (allantois and amnion) and the amniotic fluid, as essentially terrestrial reproductive adaptations. In plants, terrestrial adaptations for reproduction have been associated with the emphasis placed upon the sporophyte generation and involve the development of spores or pollen grains that are passively carried by wind, water, or insects.

The Physical Factors That Affect Organisms

In whatever medium or media the organism lives, it is subjected to a number of physical conditions and energies that not only modify and condition the medium but also govern and limit the activities of the organism. Among these factors are temperature, quantity and intensity of light, humidity, currents in the medium, the pull of gravity, the pressure of the medium, and the presence and concentrations of various chemical substances.

Temperature. Measured temperatures within our universe range approximately from absolute zero (−263°C.) to more than 6000°C. (the approximate surface temperature of the sun); but active life processes are limited to a range between a few degrees below 0°C. to some 60 or 70° above. (Quiescent states, in which an organism may survive for a time with a nearly complete cessation of metabolic processes, would extend these limits perhaps a score or more of degrees in each direction.) For any one kind of organism, these *limits of toleration* for temperature extremes are narrower, usually very much narrower, than those indicated above, and somewhere within its own specific limits of toleration, each organism has an *optimum* temperature most advantageous for its needs.

The limits of toleration and the optima of different species vary widely. Some have wide limits of toleration; others very narrow ones; for some, the limits of toleration lie within the range of temperatures characteristic of the tropics; for others, the limits are within the temperature ranges of the temperate or boreal climates. Here we find part of the explanation of the geographic distribution of numerous organisms, both plants and animals.

Temperatures also play an important part in governing the daily activities and habitat selections of organisms. This is shown if we watch an animal that is wandering at random when it encounters a difference in the temperature of its medium. If the new temperature is farther from the optimum than the old, the animal will ordinarily show an avoiding reaction and turn back or away from it; if it is nearer the optimum than the old, the animal ordinarily moves into the new situation.

Such reactions or turnings in response to temperature are typical of a large number of more or less fixed and automatic responses that organisms make to the stimuli that they receive from various physical and chemical conditions of their environment. All these automatic responses are termed *taxes*,[1] or *tropisms* (Greek, *trop*, "a turning"), and the particular turnings in response to temperature are termed *thermotropisms; negative thermotropism* when the organism turns away from a given temperature; *positive thermotropism* when it turns toward a given temperature. Thus *Epiphragma solatrix*, a cranefly found in Florida, if in a temperature of 15°C., is ordinarily negatively thermotropic to a temperature of 10°C. but positively thermotropic to a temperature of 20°C.

Humidity. Another environmental factor of much importance to many terrestrial organisms is the amount of moisture in the air. All the space occupied by air has a capacity for water vapor. (Since both the molecules of the air and of the water vapor are widely dispersed, a given cubic space, at a given temperature and pressure, has a water capacity that is independent of the air present.) When an air space contains less than its capacity of water vapor, it tends to take up water by *evaporation* from all available sources. Among such sources is the water contained in living organisms. Since organisms have very different degrees of protection against water loss, we find that they have very different limits of toleration for the water capacity of the air space about them.

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[1] Pronounced *tax-ees;* singular, *taxis.*

One of the most useful measurements of the amount of water vapor in the air is the *relative humidity.* This is a statement of the percentage of saturation with water vapor that exists for a given situation at a given time. The lower the relative humidity the more rapidly and the more powerfully will evaporation go on; the greater the relative humidity the less difficulty will an organism have in retaining its water supply. At midday during May, the various types of natural situations in northern Florida vary from a relative humidity of 15 to 25 per cent (open sand-scrub and blackjack oak habitats) to 85 to 95 per cent (below the shrubs and herbage of deep woods and swamps). The lower humidities are far beyond the limits of toleration for amphibians and many insects, and these animals show a type of *hydrotropism* that keeps them within areas of relative humidity as near as possible to their optima. Some of the lizards and insects of this region, on the other hand, are well adapted against water loss and move freely into the xeric sand-scrub areas.

Humidity and Temperature Together. So far we have considered temperature and humidity separately, and if one wished to make the simplest (and clearest) experiments on their effects on the behavior of organisms, he would attempt to hold the one constant while he varied the other in his experimental setups. In nature, conditions are generally not simple. Often, if both temperature and humidity are varying, it is impossible to be certain which is the more stimulating or limiting factor. Moreover, for a given organism the limits of toleration and the optimum for temperature change with changes in humidity, and vice versa. Man, for instance, can tolerate for several hours, at a humidity of 20 to 30 per cent, temperatures that would be quickly fatal at a humidity of 80 per cent or more. Recently, air-conditioning engineers have found that for each temperature there is a certain optimum humidity within which man is most comfortable and works with greatest efficiency; and for each temperature level, the optimum humidity lies at a different point on the scale of percentage of saturation.

Light. Aside from furnishing all the energy for photosynthesis, light has many important effects on the reactions and behavior of organisms. Many organisms have limits of toleration and optima for their various intensities, and much of the behavior of both plants and animals can be traced to *positive* or *negative phototropisms* to certain of these intensities. The positive phototropism of moths, beetles, and flies to lights at night is particularly interesting in view of the fact that nearly all these same insects show a marked negative phototropism to all but the weakest intensities of daylight. Practically all green plants show a marked positive phototropism in the direction of growth of their green parts. This is often strikingly conspicuous in plants grown indoors, and in the differences of shape that develop in two trees of the same kind when one grows in a forest and the other in an open field.

The behavior of many organisms is also influenced by the proportion of light and lightless hours in the day. This is, of course, most conspicuous in those regions of the earth where marked differences in length of day are a part of the change in the seasons. Changes from summer parthenogenesis to autumnal bisexual reproduction in certain insects and the migratory behavior of certain birds have been found to be largely regulated by changes in the relative amounts of daylight and darkness in each 24 hours.

Other Factors of the Physical Environment. Some of the ways in which temperature, humidity, and light modify the environment and influence the behavior and distribution of organisms have been briefly described. With these for examples, some of the other important factors may be even more briefly mentioned. All these (except gravity and perhaps contact) exhibit a wide range of intensities, for which organisms have various limits of toleration and optima and to which many organisms respond by positive or negative tropisms.

Pressure of the medium is of most importance to the organisms that live in the sea or in deep lakes, where some organisms are limited to the surface waters and others to various levels in the greater depths. Some of the whales appear to show the widest limits of toleration to pressure, and range from the surface to depths of several hundred fathoms. There is little evidence that air pressure, as such, is very important in setting limits of toleration for terrestrial animals, but tropistic behaviors toward varying intensities of pressure are shown by a number of forms. Reactions to pressure of the medium are termed *barotropism.*

Currents in the medium are most generally important for aquatic organisms, although a considerable number of insects show reactions to air currents. Nearly all fish automatically head into a water current, changing their positions promptly with each change in the direction of the current. This is easily demonstrated by placing a number of small fish in a pan of water and then stirring the water. If the pan contains both stream and pond fishes, it will be noted that the former usually show a much more delicate and precise reaction. Reactions to the current in the medium are termed *rheotropism*—positive if the organism faces or moves against the current; negative if it avoids or attempts to escape from it.

Various *chemicals* that are dissolved or diffused in the medium are important factors both because reactions (*chemotropism*) on the part of organisms are produced and because many of these substances may exist in concentrations above or below the limits of toleration of some or all organisms. Among the very important substances in solution in water are oxygen, carbon dioxide, various calcium salts, and hydrogen and hydroxyl ions. Less generally important but of particular interest from the standpoint of conservation are the vast quantities of sewage and of poisonous mine and factory wastes that, through thousands of miles of the streams of the United States, have come to exceed the limits of toleration of nearly all forms of life.

Contact. Numerous animals exhibit a positive reaction to contact with some comparatively stable surface. This reaction (positive *thigmotropism*) tends to keep a considerable number of invertebrates and perhaps some of the smaller vertebrates hidden in crevices or beneath protecting rocks and leaves when they are not in search of food. Nearly all the crawfishes and lobsters furnish very good examples of this type of reaction.

An interesting and characteristic society of small animals that live at the surface of quiet waters (marsh pools and small ponds) is partially to be accounted for by the positive thigmotropism of many of its members to the air-water surface film. This film is sufficiently stable to serve as a "ceiling," where small aquatic animals may cling or move about, and to serve as a floor for a rather diverse population of small arthropods.

Gravity. Many plants exhibit very clear-cut reactions to gravity. The embryonic root at germination always exhibits a very strong *positive geotropism* and "insists" on growing downward, even though the young plant is turned upside down after growth has begun. The embryonic leaf shoot, on the other hand, shows a definitely *negative geotropism* and grows upward, even if this necessitates overcoming considerable interference. In general, geotropism is more characteristic of plants than of animals, but a number of animals show a definite geotropism.

The Soil as an Environmental Complex

Soil may be defined as the layer of mixed mineral and organic material, penetrated by plant roots, that covers at least 95 per cent of the land surface. It lies at the contact of the atmosphere with the lithosphere, and is subject to repeated wetting and partial drying, to leaching in its upper layers and cementation in its middle and lower layers, to changes of temperature, and to the influences of the plants and animals that live upon and within the soil.

It would appear logical to consider the soil as one of the media in or upon which organisms live, but, unlike air or water, the soil is so complex and varies so widely from place to place that in its relationships to the organism it combines the roles of medium and modifying factors. We have already seen that the soil is the storehouse for a large list of necessities for organic life and that its characteristic biota of bacteria, fungi, and animal life has a very important part to play in the energy cycle. But just as temperature, light, and humidity may vary widely in intensity and quantity and thus produce widely different environmental conditions, the variations in soil are likewise of great importance in governing both the geographic and local distribution of organisms.

In order to appreciate the complexity of the soil and its great variability, it is necessary to know something of the parent materials and the processes and agents that produce and modify it. The most important of these are (1) the *kind of rock* from which it is largely derived; (2) the *kind of climate* (temperature, rainfall, etc.) in which it has been formed; (3) the *type of vegetation* that has grown upon it; (4) the *length of time* the weathering processes have continued; (5) its *texture* (kinds and sizes of particles); (6) *aeration and drainage;* (7) the *predominating processes* that have operated and the order in which they have occurred. We shall consider only a few of these very briefly to illustrate something of the possibilities for variation in the resulting types of soils and to point out some of the factors that result in the belts and zones of soil groups illustrated in Fig. 145.

When the surface of the land is first exposed to weathering processes, it consists either of bedrock or (very locally) of unconsolidated marine or fresh-water deposits. Under the action of wind, water, gravity, changes in temperature, and chemical solution, the rock disintegrates and crumbles into various-sized particles that may be roughly classed as gravel, sand, silt, and clay.

Gravel particles are more than 1.0 mm. in diameter.

Sand particles range in diameter from 1.0 to 0.05 mm.

Silt particles range in diameter from 0.05 to 0.005 mm.

Clay particles are less than 0.005 mm. in diameter.

As these particles accumulate, they are subjected to the action of *soil water.* If rainfall is distinctly greater than evaporation, the soluble salts of calcium, magnesium, potassium, etc., will tend to be carried *down* beyond the reach of plant roots and thus lessen the productivity of the soil. On the other hand, if the rainfall is distinctly less than evaporation, the soil water will move *upward,* and the soluble salts will accumulate on the surface, producing alkali soils that are unproductive

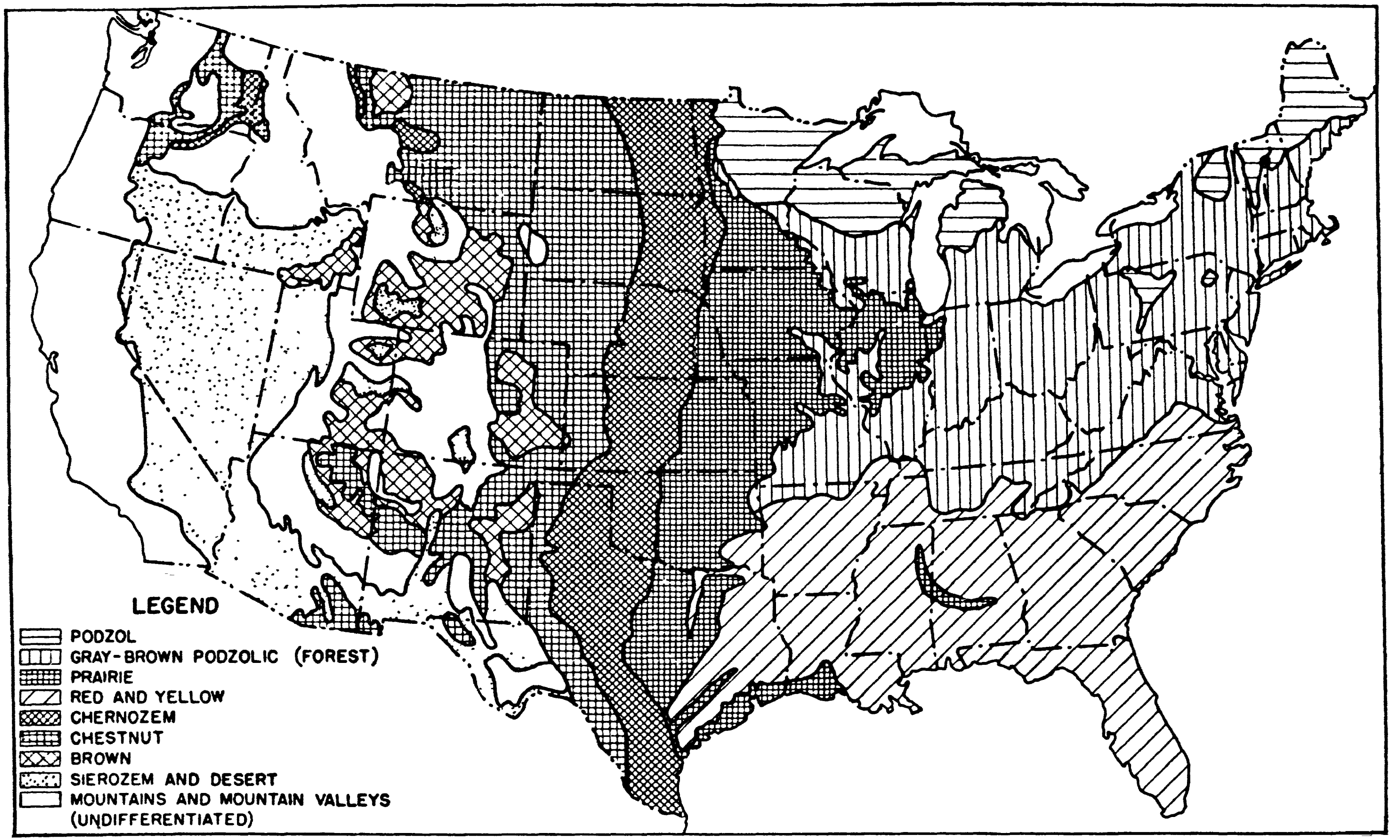
LEGEND
PODZOL
GRAY-BROWN PODZOLIC (FOREST)
PRAIRIE
RED AND YELLOW
CHERNOZEM
CHESTNUT
BROWN
SIEROZEM AND DESERT
MOUNTAINS AND MOUNTAIN VALLEYS (UNDIFFERENTIATED)

FIG. 145. *The great soil groups of the United States.* (*From U.S. Department of Agriculture, Soil Survey Division.*)

because of the too great concentration of salts and the too low moisture content. In regions where rainfall and evaporation rates are more nearly balanced, the soluble salts produced by weathering tend to remain in the soil and thus form a storehouse from which plants may freely draw. Here plant life, and consequently animal life, is abundant, and the organic accumulations from the dead bodies and the catabolic wastes of plants and animals are added to and retained by the soil.

Since the type of soil is largely determined by the climate, we find that different types of soils are characteristic of different climatic belts and zones. This is illustrated by Fig. 145. Such a map can show only the very broad and generalized regions of different soil types. Since there are many local peculiarities of climate and even more local variations in rate and sequence of soil-forming processes (because of drainage, local geological history, etc.), each of the soil areas shown on the map may, and usually does, contain numerous patches and streaks of soils that have not yet reached the typical end condition for that climate.

In general, the soils east of the Mississippi River have a low content of soluble salts, because precipitation is greater than evaporation. West of the Mississippi, evaporation soon becomes greater than rainfall (except for restricted areas in the mountains and along the Pacific Coast). In the humid regions east of the Mississippi the soils generally contain less of the soluble calcium and magnesium salts than did the parent materials, and since iron and aluminum compounds are less soluble than the calcium salts, the soil is chiefly composed of aluminum and iron compounds. In the less humid areas west of the Mississippi, on the other hand, the soluble calcium and magnesium tends to accumulate near the surface, and the soils contain a higher concentration of calcium and magnesium salts and a somewhat lower proportion of aluminum and iron compounds than the parent material.

The Chernozem, Chestnut, Brown, and Sierozem soils are all examples of the calcium-rich groups (*pedocals*); the Podsol, Gray-brown Forest, Prairie, and Red and Yellow soils are examples of the calcium-poor group (*pedalfers*). The warm and humid climate of the tropics produces zonal (climatic) soils known as *laterites*, which are particularly high in iron and aluminum.

It will be noted that there are a number of *soil groups* in both the calcium-rich and the calcium-poor classifications. This is due largely to the various kinds of ratios between rainfall and evaporation. At the one extreme, evaporation is greatly in excess of rainfall; at the other, rainfall is greatly in excess of evaporation. Moreover, some other factors enter in. The physically active parts of the soil are the humus (derived from organic materials) and clay particles. Altogether, these have an enormous surface area and usually possess electronegative charges. Consequently, they tend to hold the positively charged molecules of calcium and magnesium against the leaching effect of heavy rainfall and so keep them available for the plants. Thus it is possible for certain types of soils to be subjected to heavy rainfall and still produce a luxuriant growth of vegetation year after year. The more productive soils may be thought of as composed of relatively insoluble mineral particles coated with gelatinous organic and inorganic colloidal films to which enormous numbers of soil organisms cling.

The Prairie, Chernozem, and Gray-brown Forest soils are generally rich in soluble raw materials for food manufacture, and because of their generally favorable moisture conditions, plants growing upon them are able to utilize great amounts of the sun's energy. The dark shaded areas of the map represent the greatest *energy-capturing zones*, and it is here that we find the great grain, grass, and cattle-producing areas of the United States. The fertile lands of Russia, Argentina, and Africa lie in belts of very similar climate and soils. The once vast bison herds of North America, the huge cattle production of the Argentine, and the tremendous animal life of Africa were (or are) possible because of the luxuriant grass production in regions where abundant materials for photosynthesis coincide with an adequate supply of soil moisture.

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CHAPTER XXXVI

The Biotic Environment of Organisms

We have seen something of the diverse physical media and factors that the organism encounters, by which much of its activity and its existence is controlled. However, no organism "liveth unto itself." It has a variety of inescapable relationships with the other organisms about it, which involve various types of feeding-upon, being-fed-upon-by, competition-with, and cooperation-with activities, as well as many less obvious and less direct interdependencies. The "other organisms" include individuals both of its own species and of other species that may belong to different genera, families, orders, or phyla and often to the other organic kingdom. Some of the more conspicuous of these biotic relationships are outlined below.

The Biotic Potential. One of the very important considerations in fixing the organism's role in the plant and animal society in which it lives is its own potential reproductive rate, or biotic potential, which is, theoretically at least, a constant for a given species, dependent upon that species' inherited *sex ratio*, *number of young per female*, and *number of generations per unit of time*. It may be stated as a formula:

$$PZ^n(R^{n-1}) = \text{biotic potential (for a given unit of time)}$$

where P = number of females started with.
n = number of generations in a given unit of time.
R = proportion of females in each generation (= 0.5 when sexes are equal; 1 when all females reproduce by parthenogenesis).
Z = number of young produced by each female.

Since n and Z are theoretical maxima, they could obtain only under optimum conditions for all the factors that affect the species in question and are, at best, difficult to determine. However, sufficiently accurate approximations can be obtained to show the almost incredibly great potential reproductive ability of even slow-breeding organisms and the tremendous differences of biotic potential that exist among different kinds and groups of organisms.

Biotic Potential versus Environmental Resistance. When one calculates some of the (approximate) values for biotic potential for various organisms, it is at once obvious that no organism ever does approach its potential reproductive rate. L. O. Howard, of the U.S. Bureau of Entomology, determined the biotic potential of the common house fly (for optimum conditions, in a laboratory in Washington, D. C.), using experimentally determined values for n, R, and Z: $n = 7$ generations per year; $R = 0.5$; and $Z = 120$ eggs per female. With these values, a pair of flies should be potentially able to produce $1 \times 120^7 \times 0.5^6 = 5{,}598{,}860{,}000{,}000$ progeny in the course of a year. Actually, of course, nothing like this could happen, not because the values or calculations are false but because optimum conditions could not be maintained. Even if temperature, humidity, light, and other physical factors should stay at optimum, limits to food and space would soon produce such an intense competition that only a portion of each generation (beyond the first few) could possibly survive. Moreover, there are many organisms that feed upon flies, and not only would their toll on the population greatly cut down the number of flies that would live to produce offspring but the population of fly-eating organisms would tend to increase rapidly as the fly population increased.

Even though the biotic potential of any organism is never attained, the concept and the actual or approximate values for a given species have a much greater use than as mere exercises in arithmetic. Since the biotic potential (as an inherent maximal reproductive rate) is a constant for each species, we can use it to gain an idea of the toll that the total environment levies on that species. This is because the existing population of any species of organism (the number of bass in a given lake, for instance) is a quotient of its biotic potential and the resistance it encounters from all adverse environmental factors. It may be stated as

$$\frac{\text{Biotic potential}}{\text{Environmental resistance}} = \text{existing population}$$

Since the biotic potential may be determined (at least approximately) by experiment and observation and the existing population may be counted or estimated, we can thus obtain a quantitative measure of the total resistance of all environmental factors.

When the English sparrow was first introduced into this country, it was freed from its native (European) competitors and enemies, and for a time it multiplied at a tremendous rate. In 1889, when agriculturists and others were alarmed by its rapid increase and spread across the country, it was estimated that a single pair of English sparrows could in 10 years give rise to 275,716,983,698 descendants. Gradually this species met a stronger environmental resistance. This was partly due to the development of sparrow-eating habits by a number of our hawks, owls, and shrikes, partly to decreasing food supply brought about by changed agricultural practices and the decrease of the horse population in towns and cities, and partly (once all suitable physical environments had been occupied) to the great competition for food and nesting sites that developed within the sparrow population.

In 5 years from 1916 through 1920, the U.S. Biological Survey carried on a detailed bird census. They found that in the North Central states there was an average English sparrow population of 11 nesting pairs to 100 acres; and within this 5-year period, the population fluctuated between 9 and 13 pairs per 100 acres. According to the estimate made in 1889, each 100 acres should have produced 575 sparrows each year, but in the 5-year period studied, they were just holding their own. In the Northeastern states the environmental resistance was greater, for there the nesting pairs averaged but 5, with a fluctuation between 3 and 7 pairs per 100 acres during this same 5-year period.

Numerous examples are on record of some imported insect that, freed from its native parasites and predators, in the presence of an abundant food supply, increased at a rate that seemed comparable to the calculated biotic potential; and then, when its native enemies had been imported, became reduced to a small, stable population.

Another illustration of the relationship between biotic potential and environmental resistance is found in the sporadic outbursts of tremendous numbers of certain animals from their normal habitats and geographic boundaries, to occupy and often to become great pests in adjoining territories. Plagues of rats, field mice, and grasshoppers that arrive in countless hordes, eat the country bare of standing crops, and then move on or soon die off are well known. They illustrate the tremendous potential reproductive power that can quickly produce a thousandfold increase in a normal population whenever the environmental resistance is reduced by a few seasons of unusually favorable conditions. On a small local scale, such rapid fluctuations in the numbers of various (often nonpest) species are common and may be seen in most years in nearly any region.

Some Biotic Factors of the Environmental Resistance

We have already seen, at least by implication, that a part of the environmental resistance is due to the physical environment. Any departure from the optimum conditions of temperature, humidity, light, etc., operates to increase the time required to produce another generation and to decrease the number of offspring. We have also referred to the competition for food and nesting sites and the mortality that is caused by parasites and predators, and these last are examples of biotic factors of environmental resistance that are discussed in more detail below.

The resistance produced by the organisms that form a part of the individual's environment is in part direct and more or less evident and in part indirect and difficult to discover or evaluate. The more direct restraints placed upon an organism by the other forms of life about it are those of the predators that prey upon it, the parasites that live at its expense, and the competitors that vie with it for various limited necessities for existence and reproduction.

Predators and Parasites. By a *predator,* we mean an animal that catches and kills another animal: wolves, foxes, weasels, spiders, and snakes are familiar examples. The food strainers and trappers referred to on pages 475 and 476, and a few plants such as the bladderworts, sundews, and pitcher plants that trap animals for food, although hardly predators in the restricted sense, may also be classified here. By a *parasite,* we mean an organism that lives on or in the tissues of another organism, the *host,* feeding on the host's tissues, its digested food, or the products of its metabolism. Parasitic habits and adaptations are more varied than predatory habits, and examples of parasites include both *ectoparasites,* such as fleas and lice, and *endoparasites,* such as tapeworms, hookworms, the plasmodium of malaria, and literally thousands of other animal and plant organisms. Both the plant and the animal kingdom furnish innumerable examples of parasites and of host organisms. Plants parasitizing plants, plants parasitizing animals, animals parasitizing plants, and animals parasitizing animals are all common and well-known phenomena. Both predators and parasites take a tremendous toll of the organisms that they feed upon and tend to increase their proportionate toll whenever circumstances permit the abundance of their prey or their hosts to increase.

Competitors. Many of the necessities that any organism requires for continued existence are limited in quantity and distribution. Suitable food (or raw materials for food manufacture), nesting sites, areas in which physical factors do not exceed the limits of toleration, and refuges in which animals may escape the onslaught of their predators are all limited in amount or in extent. In any situation, some of the necessities for existence may be much less restricted than others. The necessary oxygen for respiratory needs is practically unlimited, at least in terrestrial situations, and the space in a field suitable for ant nests or gopher burrows is not badly crowded. Similarly, we find that there is much unoccupied space for grasses and herbage on the floor of a well-shaded forest, however crowded the individual grass plants may be on a lawn.

Here we see a principle in operation that is often termed *Leibig's law of the minimum.* Every organism has a rather long list of necessities, and it is *that necessity that exists in minimal quantity* that produces the most stringent competition and limits the size of population. The ant population in a field is probably limited by the food supply; and the

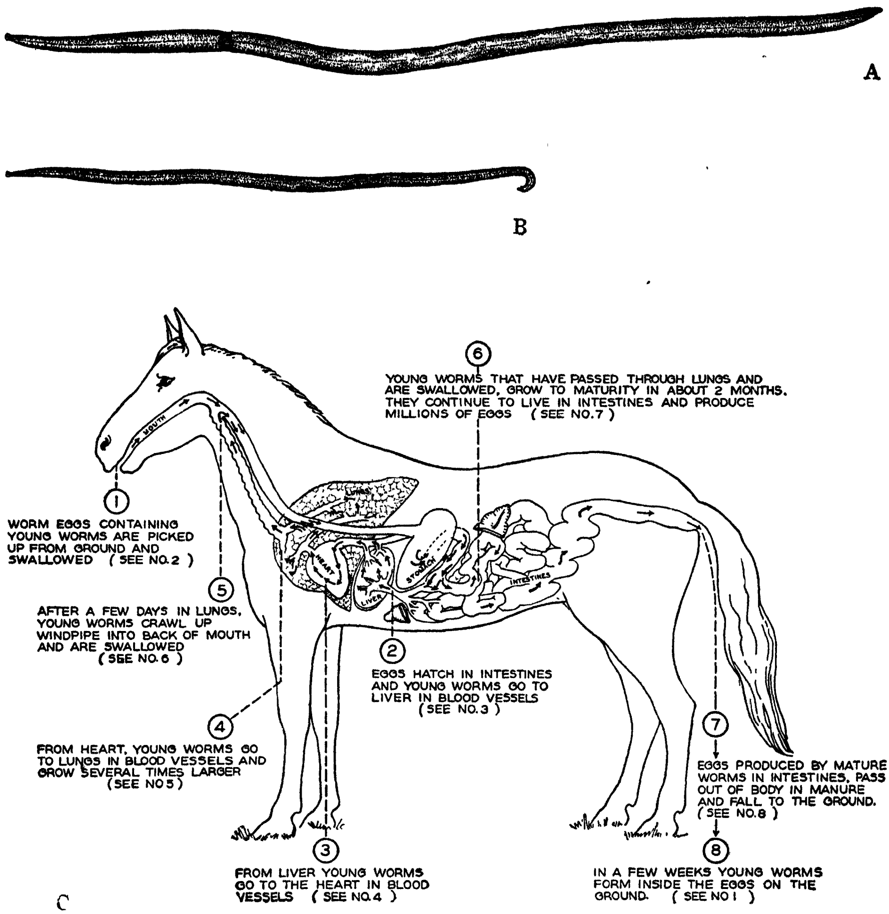
A
B
MOUTH
LUNGS
HEART
LIVER
STOMACH
INTESTINES
⑥
YOUNG WORMS THAT HAVE PASSED THROUGH LUNGS AND ARE SWALLOWED, GROW TO MATURITY IN ABOUT 2 MONTHS. THEY CONTINUE TO LIVE IN INTESTINES AND PRODUCE MILLIONS OF EGGS (SEE NO.7)
①
WORM EGGS CONTAINING YOUNG WORMS ARE PICKED UP FROM GROUND AND SWALLOWED (SEE NO.2)
⑤
AFTER A FEW DAYS IN LUNGS, YOUNG WORMS CRAWL UP WINDPIPE INTO BACK OF MOUTH AND ARE SWALLOWED (SEE NO.6)
②
EGGS HATCH IN INTESTINES AND YOUNG WORMS GO TO LIVER IN BLOOD VESSELS (SEE NO.3)
④
FROM HEART, YOUNG WORMS GO TO LUNGS IN BLOOD VESSELS AND GROW SEVERAL TIMES LARGER (SEE NO 5)
⑦
EGGS PRODUCED BY MATURE WORMS IN INTESTINES, PASS OUT OF BODY IN MANURE AND FALL TO THE GROUND. (SEE NO.8)
③
FROM LIVER YOUNG WORMS GO TO THE HEART IN BLOOD VESSELS (SEE NO.4)
⑧
IN A FEW WEEKS YOUNG WORMS FORM INSIDE THE EGGS ON THE GROUND. (SEE NO 1)
C

FIG. 146. *The relationship between the horse and one of its internal parasites, the large roundworm Ascaris. Upper two figures, the roundworm: (A) female; (B) male. Lower figure, (C) the life cycle of the parasite and its journey through the horse. (From Schwartz, Imes and Wright, U.S. Department of Agriculture, Circular No. 148.)*

severe physical conditions and low supply of raw materials for food manufacture limit the grass and herb population of an oak scrub. On the forest floor, the minimal necessity is probably light, although grasses are poorly equipped in several ways to compete with the typical forest plants.

Competition occurs both between the individuals of the same species and between individuals of different species. Because the requirements of all members of the same species are alike in practically all respects, *intraspecific* competition is particularly severe, as it is between different species that have very similar total requirements. *Interspecific* competition in most instances, however, is only partial, and each species can usually find at least restricted areas or habitats where conditions are nearer to its own optima than to those of its rivals and in which it therefore has some advantage over the latter.

Some Indirect Restraints. The indirect restraints that may be placed upon an organism by its biotic environment are variable and fluctuating but nonetheless important. Ordinarily, for instance, the martin of the Canadian coniferous forests is not molested to any important extent by the Canadian lynx that feeds extensively upon the varying hare of this region. But the hare population is subject to periodic epidemics that tremendously reduce its numbers, and at these times the martin not only finds severe competition from the lynx but is actually preyed upon by it. Another example is shown by the relationship that appears to exist between the bobwhite quail and the cotton rat of our southeastern coastal plain. Here the rats, when they are very numerous, may become an enemy of the quail through feeding upon the latter's eggs and young; but the rats are the usual and preferred food of a number of hawks and owls that do not ordinarily molest the quail to any appreciable extent. When, however, the rat population is for any reason markedly reduced, the hawks and owls that had depended upon them for a food supply turn to the quail and may become an important check upon the quail population. It would thus appear that the rat population, if it is too great or too small, affects the quail adversely; but in some intermediate (and average), size is beneficial in forming a "buffer population" that protects the quail from injurious predation by the hawks and owls. If this relationship is real—and there is much evidence to substantiate it—the various parasites that live upon the cotton rats and those that live upon the hawks and owls must also play an indirect but often an actual part in the quail's environment.

Highly probable or partly substantiated instances of such indirect relationships are very common, and there is little doubt that any form of wild life, if it were sufficiently studied, would show the same sorts of indirect dependencies upon other organisms. The complexity of these relationships, however, and the continual fluctuations in their intensity make them exceedingly difficult to demonstrate or to evaluate quantitatively.

One of the important features of all biotic resistance is that it is very variable and that it tends to become increasingly severe whenever the organism's reproductive potential is temporarily freed from some of the restraints that ordinarily hold it in check. If, for instance, any species encounters a period of particularly favorable physical conditions, the resulting drop in environmental resistance permits a prompt increase in population size. Sooner or later, a return of average or adverse physical factors would take place, but there is no causal relation between the resistance of the physical environment and an organism's population size. The biotic resistance, on the contrary, tends to increase with the organism's population size, intensifying the amount of intraspecific competition and favoring an increase in the population sizes of its predators and parasites.

This tendency of the biotic resistance to hold an organism's population size in check when the physical resistance decreases leads to some rather paradoxical relationships that appear to be rather well substantiated by field observations. There is evidence, for instance, that an extreme reduction in the numbers of an organism's normal predators may be actually harmful for it. In an environment in which food and physical factors show a wide seasonal (or other periodic) fluctuation, an organism, if freed from nearly all biotic resistance, will tend to build up so large a population size in good times that it will completely exhaust all food supplies before the next adverse season has ended. Something very like this was recently shown by the elk herd at Jackson's Hole, Wyo. Here the abnormally large summer increase in the protected elk population, freed from the normal predation of mountain lions and bears, resulted in such a large winter herd that they quickly exhausted the limited winter forage and were faced with wholesale starvation. Fortunately, in this case, the local forest rangers met the emergency by the importation of enough hay to tide the elk over until the reappearance of the next spring's abundant natural forage.

COOPERATIVE RELATIONS AMONG ORGANISMS

By no means all of an organism's relationships to the other forms of life about it are adverse or inimical; many types of interdependency involve cooperation and mutual aid. Some of these cooperative relationships are among individuals of widely different species or of different orders, classes, phyla, or even kingdoms; others are shown by the many kinds and degrees of social behavior that exist among individuals of the same species—the herds, coveys, schools, flocks, packs, and unnamed family groups that confer various sorts of mutual advantage to some or all of their members.

Cooperation among widely different forms of life shows almost every gradation from close, often obligate, partnerships in which the benefit received by each of the participants is clear-cut and unmistakable, to cases that are difficult to distinguish from true parasitism. An example of the truly mutual relationship that is termed *symbiosis* is shown by the lichens, a widespread group of lower plants in which each "individual" plant comprises an alga intimately associated with a fungus. The chlorophyll of the algal cells carries on photosynthesis, and the tissues of the fungus protect the delicate algal cells and collect and store water and minerals for their needs; both the alga and the fungus are maintained by the anabolic profits of the partnership. A somewhat similar example is shown in the relationship between many of the legumes, such as clover, alfalfa, and peas, and the nitrogen-fixing bacteria that live within their root nodules. The legumes provide protection and the requisite food supplies for the bacteria and receive, in return, a rich supply of available nitrogen for their own growth.

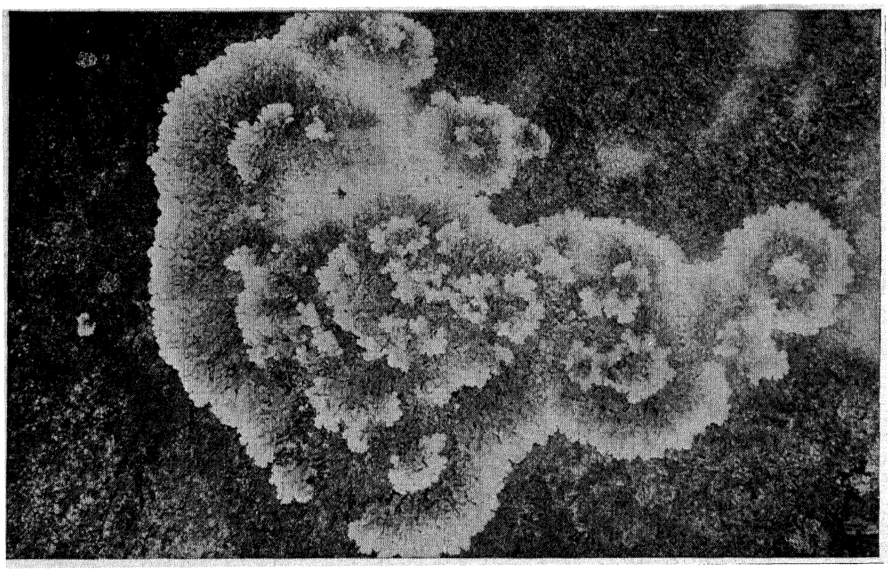

Fig. 147. *An encrusting lichen (Parnelia sp.) growing on rock, Chester county, Pennsylvania. Lichens are made up of two simple plants, one a green alga and one a fungus, growing intermingled in close symbiotic relation with each other. Lichens of this type are very characteristic pioneers on exposed rock surfaces, and by their weathering activities help to produce conditions suitable for other organisms. (Photograph by A. M. Laessle.)*

Comparable examples are also common among animals. The termites that are notorious devourers of wood are unable to digest the woody tissues that they chew and ingest. Instead, they are dependent upon the unicellular organisms that inhabit their intestines for the enzymes that will make the woody pulp available for their own tissues. A termite deprived of its intestinal symbionts will starve in spite of a plentiful supply of wood, whereas the unicellular organisms that provide the enzymes depend upon the termite for protection, moisture, and a continuous supply of wood in the proper physical condition for digestion.

Only slightly less intimate relationships exist between many species of plants and of insects. The insect visitors to flowers are rewarded by nectar or pollen that in many instances forms the insects' staple, or even sole, food supply. In return, the insect, in its journey from blossom to blossom, carries pollen from anthers to pistils and so effects the fertilization of the plant's ovules. So close is this relationship that a great many species of both insects and plants are wholly dependent upon this mutual exchange for their continued existence; and many of the specific structural characters of both insects and flowers and many of the specific psychological behaviors of insects are special adaptations to some particular insect-flower interdependency.

Many intermediate relationships also occur, in which one member receives much more than 50 per cent of the total benefit Nearly every ant and termite nest houses a number of so-called "guests" —other species of arthropods that live in the nest, and that vary in role from more or less innocuous scavengers to definite social parasites living on the food gathered by the ants for their own use, much as rats, mice, and roaches live at the expense of man. Such social parasitism, *commensalism*, may be combined with other, and symbiotic, relationships, and it is not always possible to distinguish between the two.

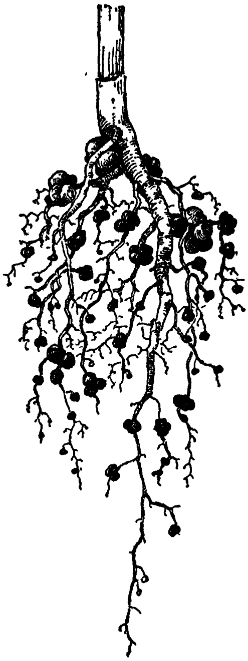

FIG. 148. *Root system of a young bean (Phaseolus), with numerous tubercles or nodules in which nitrogen-fixing bacteria live symbiotically with the bean plant. One half natural size. (From Haupt, An Introduction to Botany.)*

Another rather special type of interspecific relationship is exemplified by the "slave-making" habits of certain ants. These slave makers raid the nests of certain other ant species, kill or drive off the adult ants, and carry back to their own nests the young (pupae) of their victims. These young, when they mature, become a part of the social organization in the nests of their captors and perform a number of essential duties for the maintenance of the group.

Although cooperative relationships among individuals of the same species reach their highest development among the ants, the termites and man, representatives from nearly every order of the vertebrates and arthropods show at least some degree of social behavior. In many instances, such intraspecific cooperation is seasonal, as in the hibernating assemblages that are formed in various species of insects, amphibians, and reptiles, the winter herds of deer that band together for protection, or the wolf packs that gather for winter hunting. Other groups appear to be nearly or wholly permanent, as is the case of the beaver colonies that build and maintain dams, houses, and canals, or the prairie dogs that live in "towns" of hundreds or even thousands of individuals. Many or most of these groups are primarily family aggregations, resulting from the long-continued association of parents and offspring; others have their nucleus in a family group that has been joined by unattached individuals or smaller groups in the same area; but in all instances, the group tends to confer some type of advantage on its members that is not equally available to the isolated individual.

BIOTIC COMMUNITIES AND THEIR SUCCESSIONS

As a result of the many sorts of interrelationships that obtain between organisms and their physical and biotic environments, the plants and animals of any region tend to group themselves into a series of "biotic communities."

The simplest of these are the large number of "primary" communities that are based upon the similarity of responses shown by their members to certain intensities of various physical factors. For instance, in most creeks, the processes of stream erosion and the nature of the eroded material have resulted in an almost invariable sequence of swift, shallow riffles and deep, quiet pools. In the former, the water is well aerated and flows over a clean pebble and coarse sand bottom; in the latter, the water moves slowly past silty margins and over a mud- and silt-covered bottom.

In every *riffle*, we find a definite assemblage of organisms that are adapted by their needs and reactions to current, hard surfaces and oxygen concentration to live in riffles, and are prevented from establishing themselves in pools. All the species in these riffle communities have reactions to physical factors that are sufficiently similar to keep them confined to riffles, but they do not all have closely similar biotic relationships. Some of the members of the riffle community are various species of algae that are carrying on photosynthesis; some are animals that feed upon the algae; others are food strainers; and still others are somewhat larger animals (chiefly insect larvae) that feed upon the algae eaters and the food strainers.

Other primary communities occupy the pools; and in like manner, all types of aquatic and terrestrial situations—roadside ditches; the shores, margins, bottoms, and open waters of lakes; the soil, leaf-mold and surface strata of forests, swamps, and grasslands—have their characteristic primary communities. Various primary communities, in turn, are interrelated to form larger and more complex communities. We can recognize *stream communities* composed of the members of pool and riffle communities and of some additional organisms that are not restricted to either pool or riffle but visit and feed in both of them. In the same way, the primary soil, leaf-mold, floor, herbage, shrub, and tree-inhabiting communities of the hardwood forests combine to form a larger *hardwood forest community*, to which animals like the gray squirrel and raccoon (at least partly) belong, although they are not confined to any of the primary communities of the forest.

Food Chains. Many of the internal relationships of biotic communities are due to specific sequences of various organisms in the energy cycle. Although all animal food is dependent upon the anabolism of plants, not all kinds of animals can eat plant food. In fact, most of the plant-eating animals are adapted to feed on only a few species or types of plants, and most flesh eaters are limited to a very small list of suitable prey. Most organisms are specialists in their food habits and are confined to particular kinds and sizes of food. This results in a wide variety of food chains.

All food chains have their basis in some dependable supply of a definite type of food, either (primarily) in some continuously renewed supply of plant protoplasm or (secondarily) in some constantly accumulating supply of organic detritus such as occurs in the soil or on the bottoms of lakes, ponds, and pools. Given such a food supply, the resulting food chain is somewhat as follows:

First Link. The constantly renewed supply of plant protoplasm or the steady accumulation of detritus.

Second Link. One of a few different species of "base-industry" animals that feed upon the plant protoplasm or detritus and convert it into animal protoplasm. All base-industry animals exist in large populations and have a high biotic potential. *Example:* the "midges" (Chironomus) that feed on lake-bottom detritus and occur in tremendous numbers.

Third Link. Larger and stronger animals that feed upon the base-industry population. They are much less numerous and have a smaller biotic potential than the base-industry animals. *Examples:* the spiders, dragonflies, and robber flies that feed on midges.

Fourth Link. Still larger and stronger animals that feed upon the third link. Their size makes it unprofitable for them to hunt and eat the small midges, and they depend upon the "third link" organisms to concentrate their food into larger packages. They exist in still smaller numbers than the "third-link" organisms and have a still smaller biotic

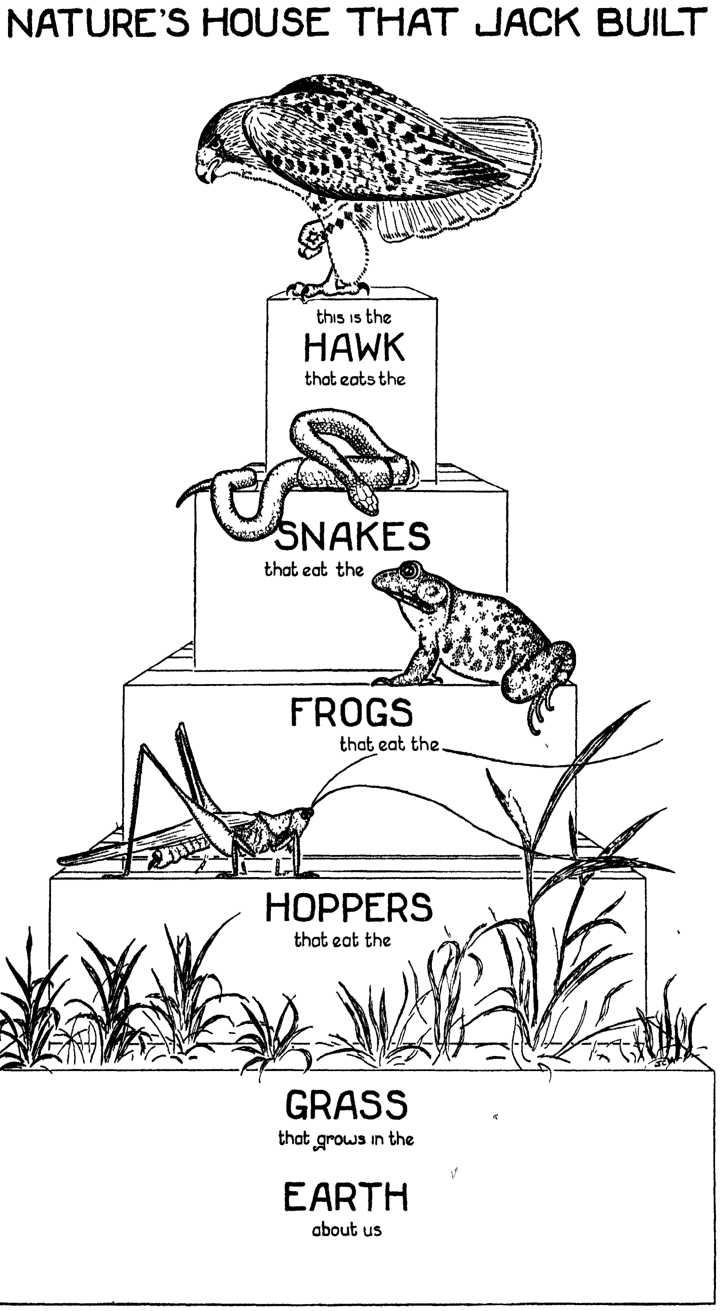
NATURE'S HOUSE THAT JACK BUILT
this is the
HAWK
that eats the
SNAKES
that eat the
FROGS
that eat the
HOPPERS
that eat the
GRASS
that grows in the
EARTH
about us

FIG. 149. *Graphic representation of food-chain relationships among organisms. Note that the chain from grass to hawks represents a "pyramid of numbers." (Based on an exhibit in the Royal Ontario Museum, Toronto, Canada.)*

potential. *Examples:* frogs and fish that feed upon spiders, dragonflies, and robber flies.

Fifth Link. Still larger and stronger forms with still smaller population and biotic potential. *Examples:* the herons and other large wading birds that live largely on frogs and shallow-water fishes.

Sooner or later, a given food chain reaches its end in animals too large and too powerful to be fed upon by other predators. (They are also too few and too slow-breeding to support another link.) The number of links will vary but in most instances will not exceed five or six. The tracing of actual food chains is greatly complicated by the existence of alternative possibilities and by the large number of possible short circuits and crossings over with other chains. Thus a fox may finally reap the benefit of photosynthesis via grass and rabbits; via grass, grasshoppers, and quail; or via plant sap, sap-sucking insects (plant lice and leaf hoppers), lady beetles, spiders, tree frogs, and snakes.

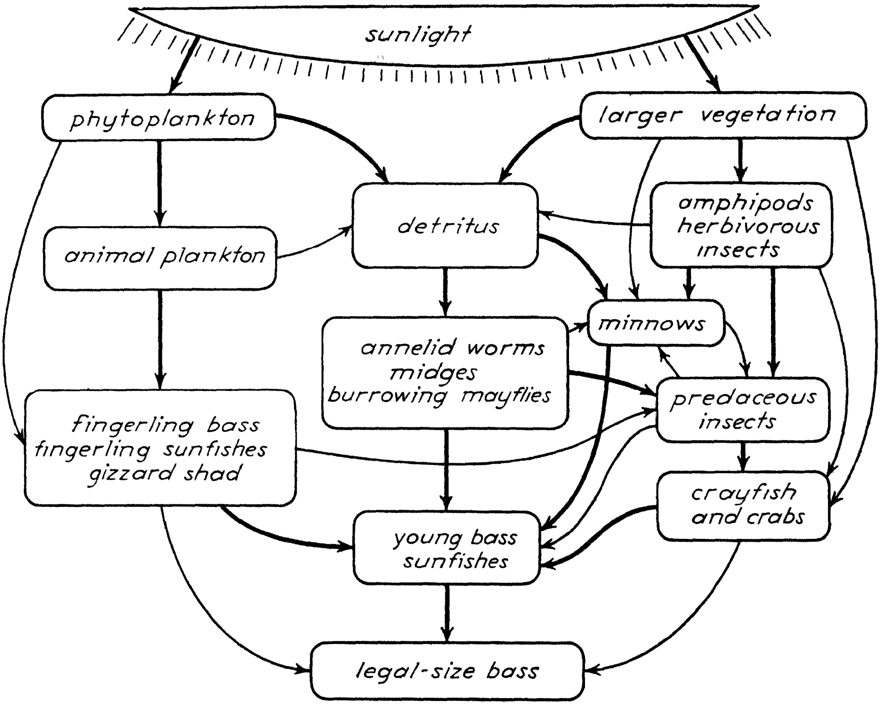
sunlight
phytoplankton
larger vegetation
detritus
amphipods herbivorous insects
animal plankton
minnows
annelid worms midges burrowing mayflies
predaceous insects
fingerling bass fingerling sunfishes gizzard shad
crayfish and crabs
young bass sunfishes
legal-size bass

FIG. 150. *Diagram of certain food-chain relationships in the St. Johns River, Florida.*

The accompanying diagram shows some staple food relations among various common groups of animals and plants in the Saint Johns River in northern Florida. The energy from the sun is captured by the photosynthesis of two great groups of plants: the phytoplankton, minute but immensely abundant microscopic algae that drift submerged through the open, sunlit waters of the river and its lakes; and the larger rooted or drifting plants of the shallow margins, bays, and inlets. The latter comprise both a luxuriant growth of submerged and emergent rooted plants and huge drifting "rafts" of water hyancinths and water lettuce. These two groups of green vegetation support large populations of "base-industry" animals and contribute large quantities of dead plant tissues to the detritus on the bottom. The latter supports a tremendous biota of bacteria, fungi, algae, protozoa, and minute crustacea that add one or two links, not indicated in the diagram, to the "detritus food chain." The arrows lead from supply to user and indicate by the various thicknesses of line the approximate importance of the relation.

Another type of food chain is found in *host-parasite relationships*. Here the progression from link to link in size, numbers, and biotic potential is just the reverse of that shown in prey and predator relationships. The parasites of the fox are smaller, more numerous, and have a higher biotic potential than the fox, and they, in turn, are hosts for still smaller, more numerous, and more rapidly reproducing parasites. Some of these relationships are just beginning to be understood, but instances of host-parasite chains of three and four links are known.

Another phenomenon that complicates the ecological relations of organisms is that known as *succession*. This is the more or less orderly progression of different types and kinds of communities that, in the course of time, come to occupy any given local area. Generally speaking, succession is brought about by two main sets of interrelated causes: local geological processes[1] and the changes in soil, water level, light, humidity, etc., that are produced by the activities of the organisms themselves.

When an area is first accessible to terrestrial or to aquatic life, it usually presents a rigorous and difficult environment, with meager food supplies and severe physical resistance. Thus the sand dunes that form on the leeward sides of many sandy lake and ocean shores are at first mere sand ridges, lacking in many of the soil substances required by most rooted plants, subject to extreme fluctuations in temperature, often desertlike in the lack of available moisture, and still liable to "blowouts" that expose roots at one point and bury entire plants at another. Very few organisms can endure such violent factors, but certain drouth, heat, and wind-tolerant species are able to form a "pioneer community" here, where they are free from the biotic resistance of less hardy competitors. In time, however, as the pioneer community establishes itself, it begins to effect changes in its environment. Organic material accumulates in the soil and thus provides more soil nutrients and retains more soil moisture; shade is provided, and the extremes of light and heat are thereby reduced; and the sand becomes anchored by the roots of the pioneers and ceases to drift with the wind. Now other plants and animals can invade the area; they were unfitted to exist under the extreme pioneer conditions but once they can find a foothold are better adapted to the increasing biotic competition. In time, the newcomers will replace the members of the pioneer community and, as they continue to occupy the area, produce a deeper, more organic, and moister soil, a

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[1] Stream erosion with the production of new-made bars, banks, cliffs, and changes in gradient; the shore deposits of lakes and oceans—bars, spits, dunes, and coastal flats; the formation and the extinction of lakes, etc.

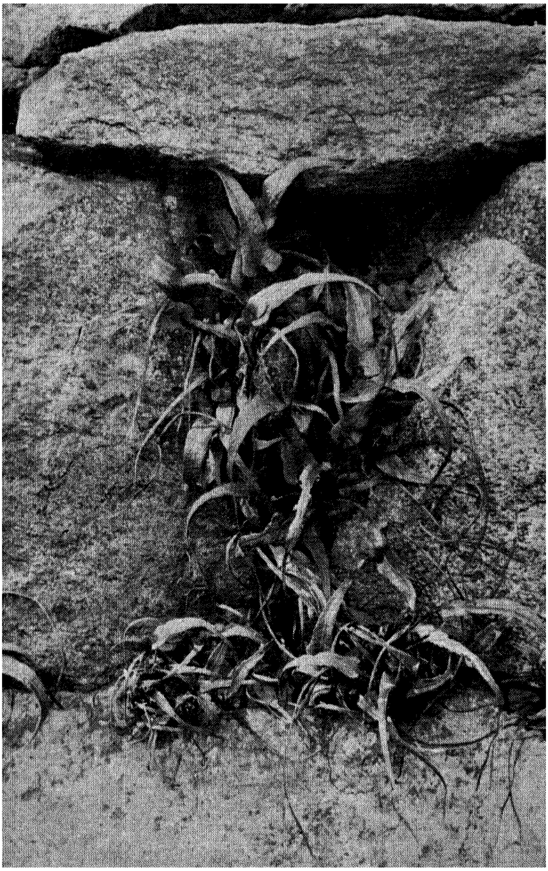

FIG. 151. *The walking-fern (Camptosaurus rhizophyllus) growing in a rock crevice, Chester County, Pennsylvania. This pioneer plant is able to endure the severe environmental conditions provided by rocky cliffs and outcrops where they are more or less moist and partially shaded. (Photograph by A. M. Laessle.)*

denser shade and more humid atmosphere. These are, in turn, supplanted by another complex of organisms still better fitted to survive and reproduce in the increasingly intense biotic competition of the ameliorated physical environment.

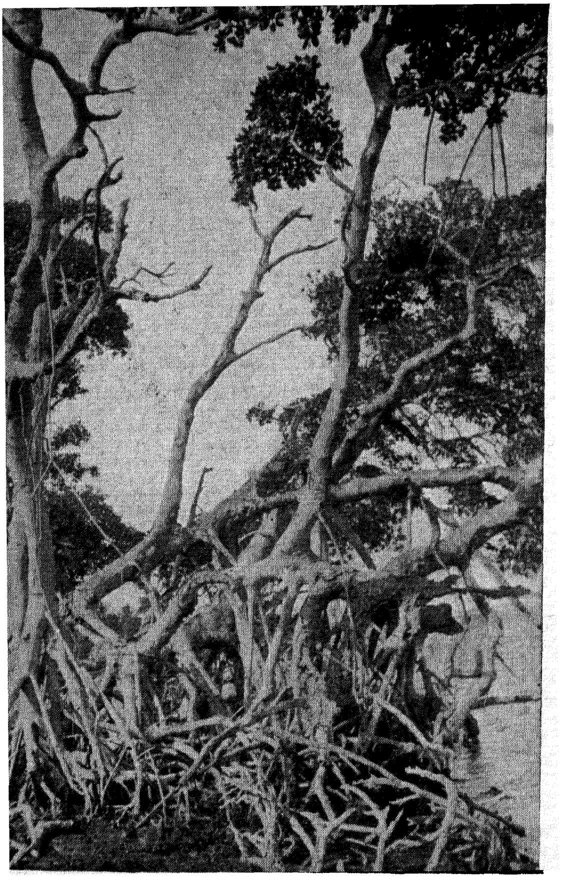

FIG. 152. *The red mangrove (Rhizophora mangle) growing on the shore of Biscayne Bay, near Miami, Florida This is the dominant plant of a pioneer community characteristic of muddy, shallow seashores of tropical and subtropical parts of America. The tangled mass of roots breaks the force of the waves and holds silt, building the shore outward; and the spike-like seedlings drop from the overhanging branches root first into the mud, thus planting themselves and extending the mangrove thicket on its seaward side. (Photograph by A. M. Laessle.)*

These successive changes are not unending. In time, the area will become suitable for invasion by a group of plants and animals that, although they may continue to effect some changes in soil, shade, humidity, and other conditions, are fitted to maintain themselves in the environment they produce. Such a community is termed a *climax* and is stable and self-maintaining so long as the general climatic conditions of the region—the average seasonal rainfall and average seasonal temperatures —do not change. In the region that surrounds the southern half of Lake Michigan, for example, the climax community is a deciduous forest dominated by beech and sugar maple.[1] By no means all of this region had developed beech-maple forests or had reached this stage before modern civilization had destroyed most of the forests. The time required for the completion of successional changes within a stable climate probably ranges from several hundred to many thousands of years, depending upon the kinds of areas that were originally available to the various

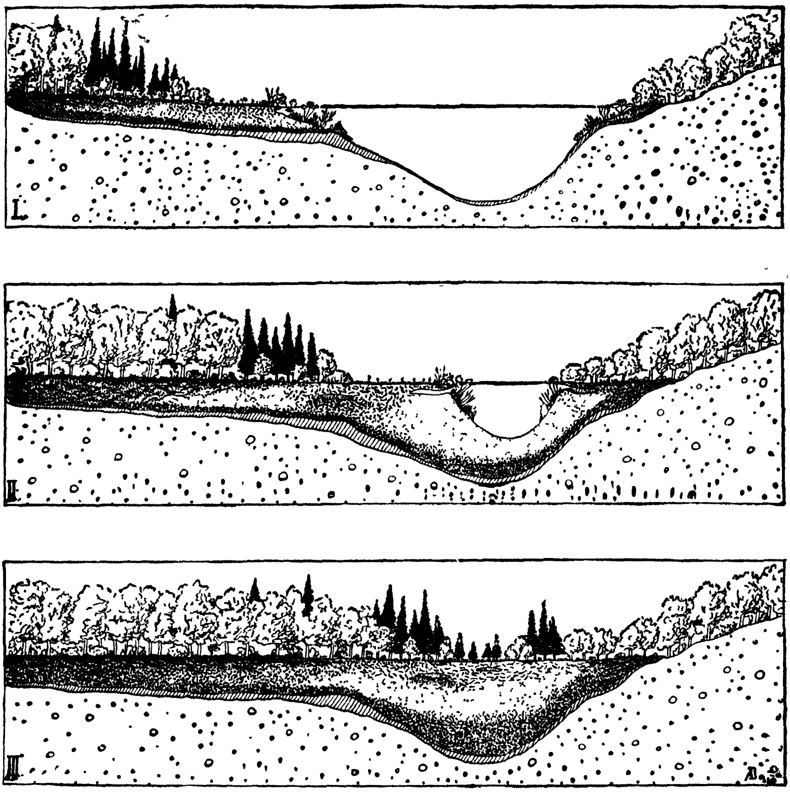

FIG. 153. *The filling of a lake with peat deposits. The succession of land plants is also shown.* (*From Shull, Principles of Animal Biology.*)

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[1] Actually this community comprises a considerable number of characteristic plants and animals, but it is the beeches and maples and a few other trees that largely determine the peculiar complex of physical and biotic factors to which all the members of this community are adapted.

types of pioneer communities, the length of the growing season, and the nature and rate of local geological processes. We know that the present climate of the region about the southern half of Lake Michigan is geologically very recent, perhaps too recent to have permitted the slower successional sequences to have developed to a climax community; moreover, local geological processes are continuously providing new situations for pioneer communities or are retarding or setting back the potential successional sequence.

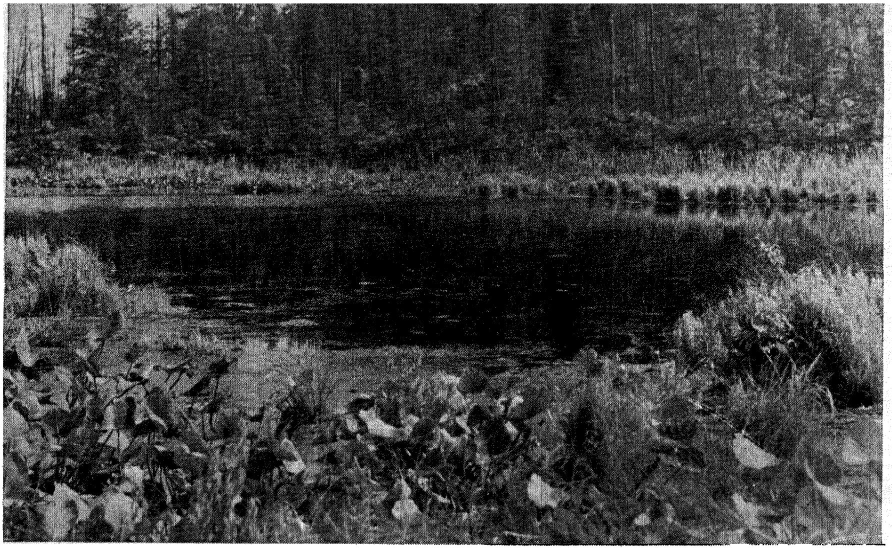

FIG. 154. *A stage in the extinction of a small glacial lake in southern Michigan. The lake, which formerly occupied the entire basin, has been almost filled in by the accumulation of plant debris and soil washed down the surrounding slopes. At the edge of the open water is a zone of rooted aquatic plants with emergent leaves—a typical pioneer aquatic community. Later successional stages are represented by the dense semifloating mat of sedges, herbage, and low shrubbery outside the zone of aquatics, and by the bog forest of tamarack, poison sumac, and other woody plants seen in the background. Eventually the entire lake basin will be covered by such a forest. This, in turn, will be replaced by other types of forest spreading in from the margins of the swamp, until theoretically the area should eventually attain the beech-maple climax stage. (Photograph taken on the E. S. George Reserve, Livingston County, Michigan, by J. S. Rogers.)*

New sand dunes, for instance, continue to form along the southern and southeastern shores of the lake and as they gradually move inland, until stabilized by the sand-dune pioneers, destroy areas of late-stage succession on parts of the earlier dunes and produce new ponds and marshes by damming the former drainage. Elsewhere, stream erosion is producing new sand bars and mud flats or exposing new clay banks or rocky cliffs; and the dwindling lakes of a former geological period still present shore lines and shallow basins for occupancy by the pioneer communities of a successional sequence that will finally cover even the lake basins with a beech-maple forest. Every type of area newly available for terrestrial life has its own special group of pioneer organisms, and the successive stages in each sequence are more or less specialized and predictable. The pioneers and subsequent sequence of communities that change a dry, wind-swept, sandy ridge into a moist, densely shaded forest are, of course, very different from those that change a lake or pond into the same sort of beech-maple climax, and both of these differ from the sequences that lead to the climax from a rocky cliff or from the bare, muddy margins of a stream.

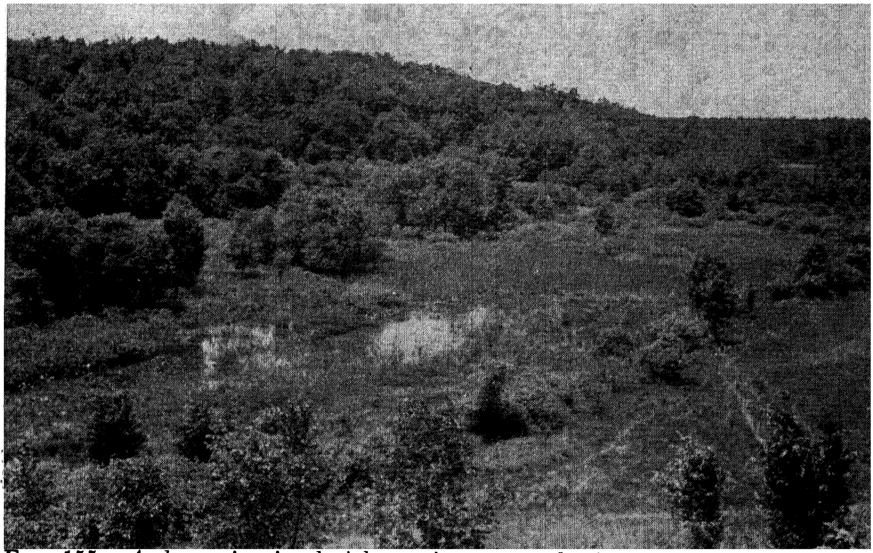

FIG. 155. *A depression in glacial moraine topography in southern Michigan, once occupied by an arm of a small glacial lake. Zonation of plant communities is clearly shown—sedge and cattail communities in the marsh, bordered by thickets of willows and other shrubby trees, and on the slopes at the left a rather dry oak-hickory forest community. None of the area shown has yet reached the climax, but eventually both the wet depression and the drier hillsides should, by different series of successional stages, become covered with the climax beech-maple forest. (Photograph taken on the E. S. George Reserve, Livingston County, Michigan, by J. S. Rogers.)*

We have used the ecologically classical "Chicago region" as a basis for our brief discussion of succession,[1] but in a region as large and varied

[1] Because of the early and important work of Prof. Cowles and his students, of Dr. Shelford and others and partly because the exceptionally fine sequence of very

as the United States, with so many types of climates, scores of different regional climaxes exist. Each has its own more or less typical successional stages, which lead from the various pioneer situations to the local climax. Westward from the Chicago region, as changes in the amount and seasonal distribution of rainfall are encountered, the climax community becomes an association of prairie grasses; and still farther west, it is an association of Great Plains bunch grasses. Southward, in the Eastern states, other hardwood trees replace the beeches and maples as dominants of the climax deciduous forest, and in northern Florida the climax association is a broad-leaved, evergreen "hammock," dominated by magnolia, holly, red bay, and laurel oak.

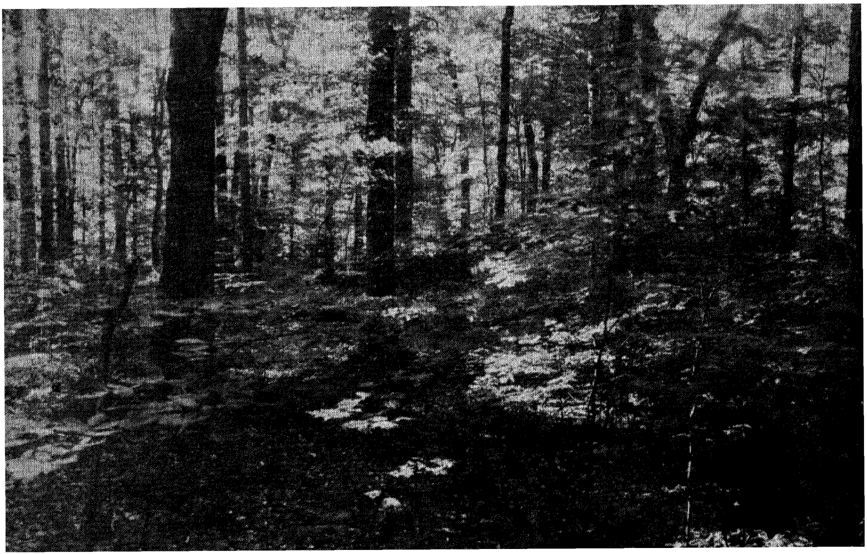

FIG. 156. *The beech-maple climax forest of the southern Great Lakes Region. (Photograph taken on the E. K. Warren Preserve, Berrien County, Michigan, by J. S. Rogers.)*

Succession in northern Florida provides a good illustration of the not uncommon circumstance in which, because of special conditions, some preclimax community attains a semipermanence or permanence and, in effect, becomes the actual climax. Such a conditional permanence appears to hold for the longleaf pine forests so long as they are periodically subject to fires. The latter are typically ground fires that destroy the invading underbrush, the forerunners of the hammock community, and so maintain the open, wind-swept, sunny forest floor that the pine

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young to old dunes in northern Indiana and southwestern Michigan so clearly shows all the stages of sand-dune succession.

requires for the growth of its seedlings. Throughout historic times, the frequent burning (at least once in every few years) of the pinewoods to provide better pasture has been a standard and well-nigh universal practice; and there is reason to believe that such periodic burning, both by prehistoric Indians and as a result of lightning, has long operated to maintain the pine-dominated communities. Today it is known that the elimination of fire allows the pine forests to be replaced by hardwood hammocks, and it seems evident that existing hammocks either owe their development to some natural barriers that protected them from fires or were developed from such preceding communities as swamps and seepage thickets.

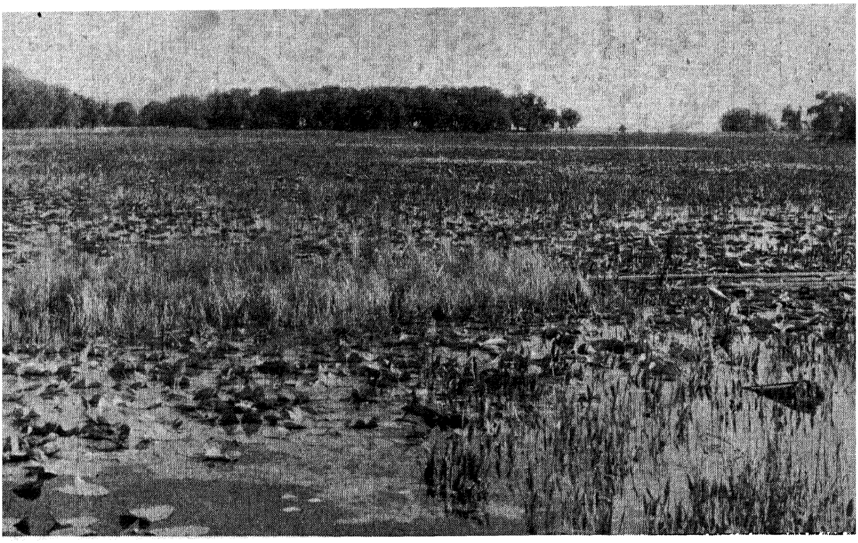

FIG. 157. *A "wet prairie" in northern peninsular Florida, densely occupied by pioneer communities of floating and of rooted emergent plants. In the background can be seen a live-oak "hammock" community. (Photograph taken near Gainesville, Fla., by J. S. Rogers.)*

Some special phases of succession are so rapid that one may actually follow them in detail. An infusion of dried grasses in water quickly develops a huge population of bacteria, and within a few days, one or more species of protozoa (introduced with the dried grasses or air-borne with dust particles) appear, feed upon the bacteria, and multiply at a prodigious rate. Then, within a few more days, other species of protozoa appear, and the earlier species wane. This process may continue, each form producing biotic, chemical, or physical changes in its environment that pave the way for some succeeding form, until a sequence of perhaps a dozen species will occur within the space of a few weeks. A similar but somewhat slower succession can be seen in the stages of decay of a fallen tree. Within a few years—the number depending upon the kind and size of tree and the place where it falls—it will have changed from sound wood to a moldering heap of humus and in the process will have formed the habitat of a number of successive microcommunities, each dependent

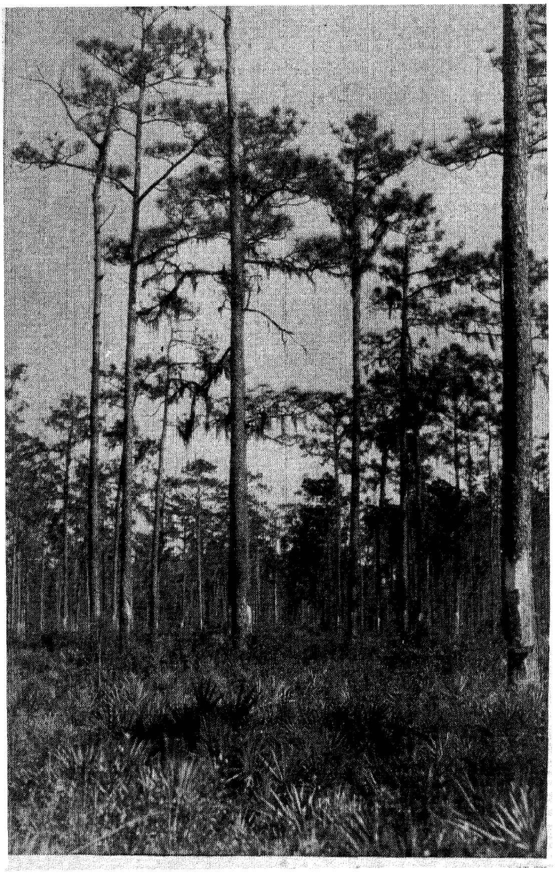

FIG. 158. *A persistent subclimax association maintained by recurrent fires—a longleaf pine "flatwoods" in northern Florida. This type of flatwoods is characteristically developed on Leon soils, in which there is an impervious hardpan at shallow depth, causing the soil above this layer to fluctuate from very wet in rainy periods to extremely dry in times of drought. In consequence the herbage and shrubs of the lower strata and of the forest floor comprise only species able to survive in this rigorous environment with its extreme variation in water conditions If fire is kept out, these flatwoods undergo succession toward the climax association, a broad-leaved evergreen "hammock"; but fire is a normal and frequently recurring agent in most of the flatwoods areas. (Photograph by J. S. Rogers.)*

upon some particular stage in the decay of the log and each tending to destroy its own environment and make conditions favorable for its successors.

Since all succession is the result of the dynamic relations among populations and many kinds of intricately interrelated organisms, it exhibits many details, modifications, and local variations that cannot be considered here. It should be apparent, however, that the activities of civilized man, with his crop plants and his herds, his abandoned fields, his cutover forests, roadsides, his drainage and irrigation projects, and his damming and pollution of streams, intrude on a huge scale into natural successional sequences. These intrusions do not eliminate succession, but they do profoundly modify it, introduce new stages and

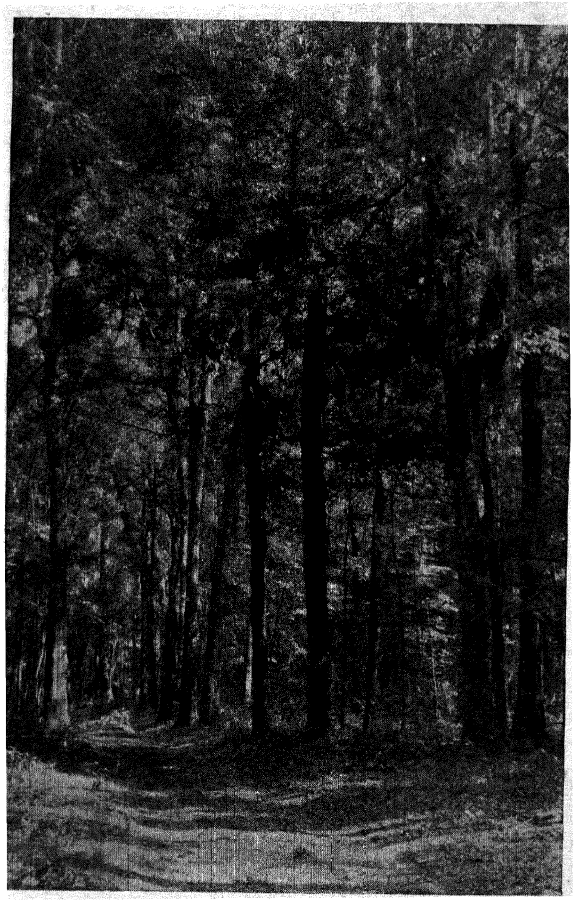

FIG. 159. *The climax association of northern Florida—a broad-leaved evergreen "hammock" dominated by magnolia, holly, red bay, and laurel oak. (Photograph taken in Alachua County, Florida, by J. S. Rogers.)*

new communities, set back or advance the progress of natural stages, and even change the local type of climax, toward which the region trends. Not a few of man's modifications have proved unfortunate for his own long-run and even comparatively immediate needs, and it is becoming increasingly clear that a knowledge of the interdependencies of organisms and communities and of their successional relations is highly necessary for any rational and efficient maintenance and long-continued use of the world's natural biotic resources.

APPENDIX A

A Survey of the Kinds of Organisms

THIS book deals with those broad aspects of life that help us to understand man as an organism and to appreciate the various relationships that exist among all forms of life, including man. In attempting to arrive at valid and significant conclusions about life in general, we have had to consider many particular examples and kinds of organisms; for "life" as such is a mere abstraction, there being no life save in the form of real individuals that belong to particular species and to definite social complexes. We are not especially concerned with the classification of animals and plants, except as this classification enables us to see where the examples that we have used stand in relation to other forms of life. However, a survey of plants and animals such as is given here has another value, in that it furnishes us with a panoramic view of the results of organic evolution.

The background for this survey is contained in the main portions of this book. We have reviewed the major patterns of organization in our study of the structure and functioning of the individual. We have found that homologies in adult and embryonic structures afford a basis for natural classification based on blood relationships. The principles of classification and the methods of naming organisms[1] have been treated in the section on Evolution. Here we shall survey many of the actual patterns into which living things have been molded by the process of evolution, arranged so far as possible in phylogenetic sequence. This appendix is designed primarily for reference, but it should not on that account be deemed an unimportant part of the book. Knowledge of the principal groups of animals and plants is essential to an understanding of much of the subject matter with which we are concerned.

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[1] In the system of classification used by the biologist, the major divisions, or *phyla*, are subdivided into *classes*, classes into *orders*, orders into *families*, families into *genera* (singular, *genus*), and genera into *species* (singular, *species*). The technical name of any organism consists of the generic name plus the species (specific) name.

THE PLANT KINGDOM

For the sake of simplicity and consistency, we shall call the primary divisions of the plant kingdom *phyla*, giving the term the same meaning that it has in the classification of animals. Botanists often use *phylum* in other senses, and in botanical nomenclature, the major subdivisions of plants are called sometimes *divisions*, sometimes *subkingdoms*, and sometimes by still other names.

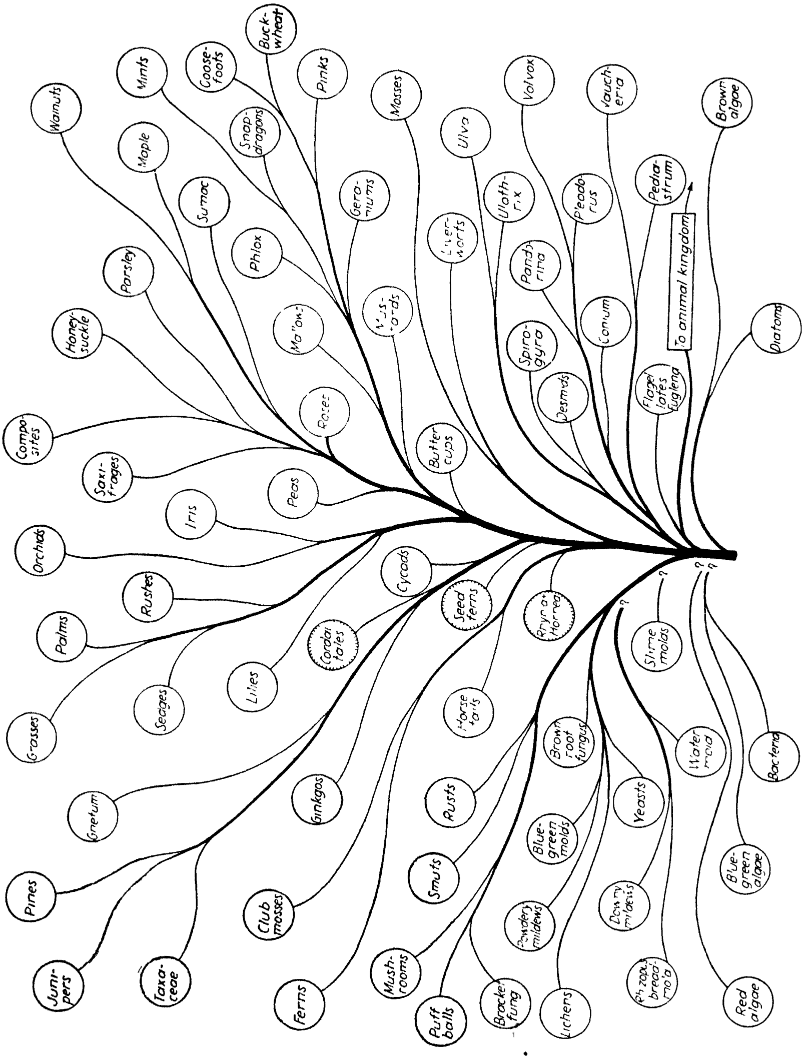

Walnuts
Mints
Goose-foots
Buck-wheat
Pinks
Mosses
Volvox
Vauch-eria
Brown algae
Maple
Snap-dragons
Ulva
Pedia-strum
Sumac
Gera-niums
Uloth-rix
Pleodo-rus
Liver-worts
Phlox
Parsley
Pando-rina
To animal kingdom
Honey-suckle
Mallows
Conium
Spiro-gyra
Desmids
Flagel-lates Euglena
Diatoms
Compo-sites
Roses
Butter-cups
Saxi-frages
Peas
Iris
Orchids
Cycads
Rushes
Seed ferns
Rhynia-Hornea
Slime molds
Cordai-tales
Palms
Lilies
Sedges
Horse-tails
Grasses
Brown root fungus
Water mold
Bacteria
Gnetum
Ginkgos
Rusts
Yeasts
Blue-green molds
Pines
Smuts
Club mosses
Powdery mildews
Downy mildews
Blue-green algae
Juni-pers
Taxa-ceae
Mush-rooms
Ferns
Puff balls
Bracket fungi
Lichens
Rhizopus bread mold
Red algae
?
?
?
?

FIG. 160. *A phylogenetic diagram of the Plant Kingdom.*

Characteristics Used in Classifying Plants. Certain features are more useful than others for classifying plants according to degrees of relationship. The more important of these are indicated below. It should be pointed out, however, that the value and applicability of these characters varies from group to group.

1. *Cell Structure.* One of the simplest groups of plants (the blue-green algae) is made up of cells which with few exceptions have no nuclei. There is considerable reason to believe that they are rather closely related to the bacteria, which also lack definite nuclei. Other instances of likeness in cell structure are similarly interpreted as indicative of relationship.

2. *Arrangement of Cells.* In some of the very simple plants, every cell division is followed by separation of the daughter cells, so that each plant consists of a single cell. In others, the cells remain together in pairs; or larger numbers of cells form accumulations that may be arranged into filaments, sheets of cells, or three-dimensional cell groups of various shapes. Although all these types of cell arrangement are found in several rather distantly related groups of thallophytes, within each of these groups they often indicate relationship of species and genera.

3. *Presence or Absence of Particular Organs or Tissues.* Whole plant groups may be characterized by the presence or absence of some particular vegetative organ or tissue. Thus the presence of true roots in all modern pteridophytes is an indication that these plants are more closely related among themselves than are any of them to the mosses or other rootless plants; it likewise indicates a closer degree of relationship to the spermatophytes (which also have roots) than to the groups of plants in which roots are lacking. Again, the absence of tracheal tubes (vessels) from the wood of most gymnosperms indicates that these plants are more truly related among themselves than they are to the angiosperms, in which tracheal tubes occur.

4. *Similarity of Reproductive Structures.* Throughout the plant kingdom, the reproductive mechanism, including the structure of the reproductive organs, affords one of the best and most used means of determining relationships. The vegetative structures are much more likely to show adaptive modifications to unlike modes of life. Thus among the closely related oaks, one species may be a large forest tree and another a spreading shrub with underground stem, but both have very similar flowers and fruit. The reproductive structures show a wide variety of characteristics—such as differences in number and arrangement of flower parts—that are little affected by the environment and yet are so modified from group to group and from species to species that they afford excellent indications of relationship.

The following table gives a scheme of plant classification which, though somewhat oversimplified, is easier to grasp than a fuller and more exact one. Groups that are starred are extinct.

The Plant Phyla and Some of Their More Important Subdivisions

Phylum I. THALLOPHYTA. The simplest plants. Body a thallus without true roots, stems, or leaves. Mostly microscopic or of small size. A large and heterogeneous assemblage.

Class 1. The Algae. Possessing chlorophyll; mostly aquatic.

Cells without definite nuclei or chloroplasts:

Subclass 1. The Blue-green Algae (Cyanophyceae).

Cells with definite nuclei and chloroplasts:

Subclass 2. The Green Algae (Chlorophyceae).

Subclass 3. The Brown Algae (Phaeophyceae).

Subclass 4. The Red Algae (Rhodophyceae).

Class 2. The Fungi. Lacking chlorophyll; saprophytic, parasitic, or symbiotic with green plants.

Subclass 1. The Slime Molds (Myxomycetes).

Subclass 2. The Bacteria (Bacteria); actually related to the blue-green algae.

Subclass 3. The True Fungi (Eumycetes).

(The Lichens are symbiotic associations of true fungi and green algae.)

Phylum II. BRYOPHYTA. The liverworts and mosses. Small terrestrial plants imperfectly adapted to land life; body a simple or modified thallus, with rhizoids and often with leaflike organs but without true roots, stems, or leaves. Alternation of generations invariable, the sporophyte being parasitic on the gametophyte.

Class 1. The Liverworts (Hepaticae).

Class 2. The Mosses (Musci).

Phylum III. PTERIDOPHYTA. The ferns and fern allies. Terrestrial plants; body small to large, differentiated into true roots, stems, and leaves, with well-developed vascular system. Alternation of generations the rule, the sporophyte dominant and independent of the small, free-living gametophyte.

*Class 1. The Ancestral Pteridophytes (Psilophytales). The simplest vascular plants, known only as fossils from the Devonian.

Class 2. The Horsetails and their Allies (Equisetales). The modern Horsetails, and extinct treelike forms of the late Paleozoic (*Calamites, etc.).

Class 3. The Club Mosses and their Allies (Lycopodiales). The modern club mosses and ground pines and extinct treelike forms of the late Paleozoic (*Lepidodendron, *Sigillaria, etc.).

Class 4. The Ferns (Filicales).

Phylum IV. SPERMATOPHYTA. The seed plants. Primarily terrestrial; body with roots, stem, and leaves; vascular system highly developed; differing from pteridophytes in producing *seeds* and in having a *pollen tube*. Gametophyte generation greatly reduced, the male and female gametophytes represented by small groups of cells enclosed by and dependent upon the sporophyte tissues.

Class 1. THE GYMNOSPERMS (Gymnospermae). The conifers and their allies; seeds borne naked on the surfaces of cone scales.

*Subclass 1. The Seed Ferns (Cycadofilicales). The most primitive spermatophytes; known as fossils from the late Paleozoic.

Subclass 2. The Cycads (Cycadales). The most primitive living spermatophytes.

Subclass 3. The Maidenhair Trees (Ginkgoales). The gingko, or maidenhair tree, is a lone survivor of this group, common during the Mesozoic.

*Subclass 4. The Large-leaved Evergreen Trees (Cordaitales). Extinct, Devonian to late Paleozoic.

Subclass 5. The Conifers (Coniferales). The needle-leaved evergreen trees.

Class 2. THE ANGIOSPERMS (Angiospermae). The flowering plants. Seeds enclosed in an ovary. The dominant group of modern plants.

Subclass 1. The Monocotyledons (Monocotyledones). Seeds with one cotyledon, etc.

Subclass 2. The Dicotyledons (Dicotyledones). Seeds with two cotyledons, etc.

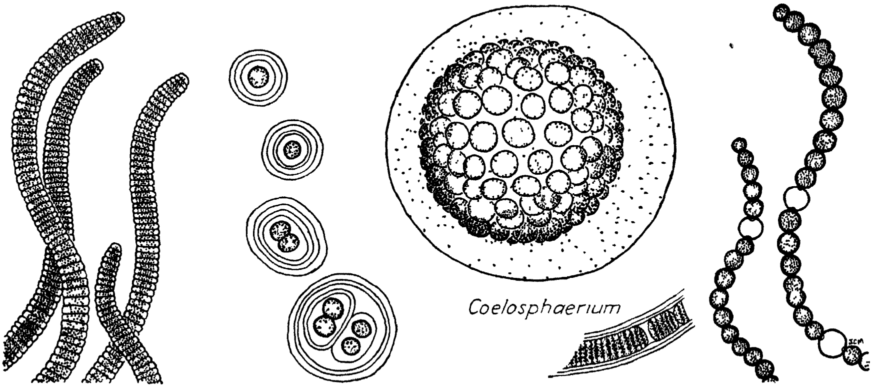
The most important characteristics of the four plant phyla have already been described and discussed in the section on the major patterns of plant life (Chap. XV). Here these features will merely be recapitulated, and our attention will be given chiefly to the principal subdivisions of these phyla.

Phylum I. Thallophyta (tha lŏf′ it a), Greek, *thallos*, young shoot, frond; *phyton*, plant.

The thallophytes (thal′ o fīts) are the simplest plants, unicellular, or with a body composed of simple, relatively unspecialized cells that form a thallus. Including the unicellular Protophyta (pro tŏf′ it a), the phylum comprises some 84,000 species, which may for convenience be divided into two artificial groups, the *algae* and the *fungi*. Those which possess chlorophyll and carry on photosynthesis form the first group; those which lack chlorophyll and which must therefore, like animals, secure their food ready made from other organisms constitute the second. Both algae and fungi include unicellular and multicellular organisms, and each group is divided into several distinct structural and functional types.

Class 1. Algae (al′ jē). Seaweeds, pond scums, and a host of microscopic forms are comprised in the 14,000 species that make up this group. All its members require abundant moisture and either are aquatic or, if terrestrial, are confined to moist situations. All the typical algae possess chlorophyll, but, in addition, the various groups have other pigments of unknown function, which give them characteristic colors. This, together with differences in reproduction and in the structure of the thallus, makes it possible to distinguish four subclasses of algae.

The *blue-green algae* consist of single cells or of colonies of similar cells surrounded and held together by a gelatinous sheath. The cells differ from those of all the higher plants and the other algae in having no clearly defined nucleus; instead, there is merely a clearer central portion of the protoplasm that apparently has some of the functions of a nucleus. Cell division in this group takes place by simple fission—a process rare in higher forms. Because of their simple cell structure and because they store their food in the form of glycogen instead of starch, the blue-green algae are thought to be only distantly related to most other forms of plant life. It may be that in them we have the simplest and most primitive of living things.[1] Blue-green algae are abundant in fresh water, especially in swamps and ponds; they also occur on moist surfaces of soil, rocks, and tree trunks.



Oscillatoria *Gloeocapsa* *Plectonema* *Nostoc*

FIG. 161. *Some blue-green algae.*

The *green algae* include unicellular and colonial motile forms that swim by means of flagella or cilia and also nonmotile forms that range in type from single cells to cell colonies of spherical, leaflike or filamentous form. Most of them are greenish yellow in color, because of the presence of a yellow pigment in addition to chlorophyll. Some of the motile forms have a red or brown pigment spot that is sensitive to light, called the eyespot.

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[1] The bacteria, a group of fungi, are even simpler in structure, but because they lack chlorophyll and, except for a few atypical groups, are not self-sustaining, they are often regarded as specialized by degeneration and hence as of later origin.

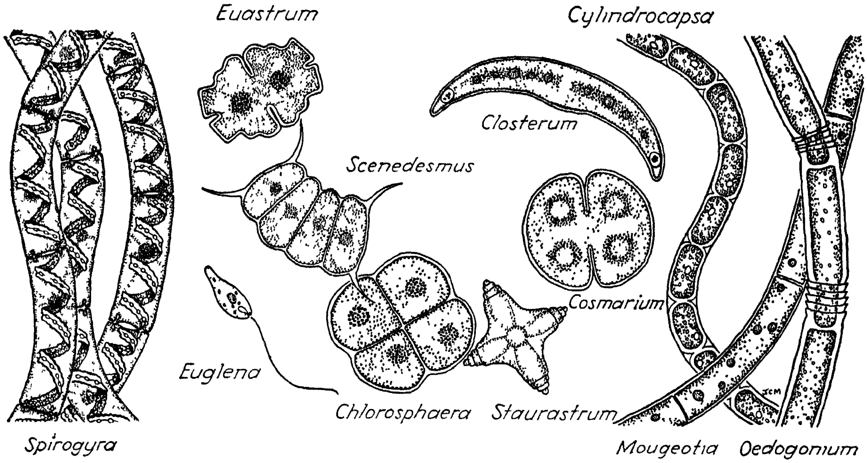
Euastrum
Cylindrocapsa
Closterum
Scenedesmus
Cosmarium
Euglena
Chlorosphaera
Staurastrum
Spirogyra
Mougeotia
Oedogonium

FIG. 162. *Some green algae.*

The members of this group are largely inhabitants of fresh water, though some live in damp terrestrial situations. In many respects, the green algae resemble the higher plants and differ from the blue-green algae. Among the characters that the green algae share with the higher plants are cells with distinct nuclei, chlorophyll that is apparently identical and similarly contained in chloroplasts, a cellulose cell wall that is structurally similar, and starch instead of glycogen produced as a food reserve.

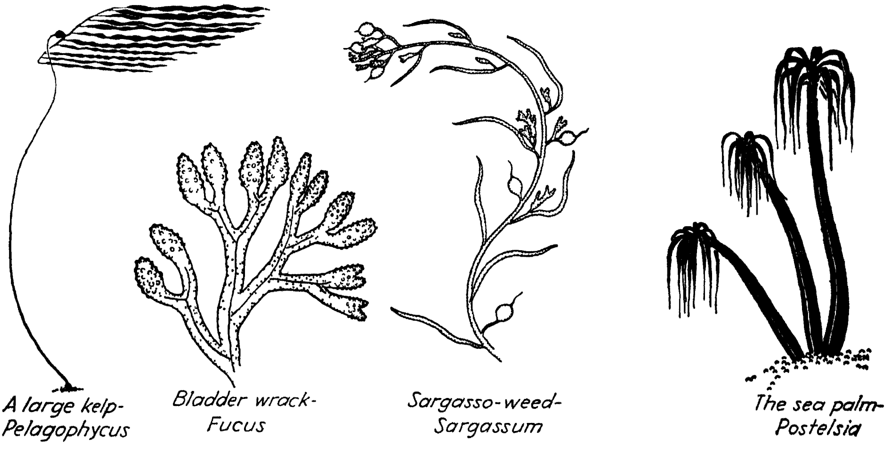
A large kelp-
Pelagophycus
Bladder wrack-
Fucus
Sargasso-weed-
Sargassum
The sea palm-
Postelsia

FIG. 163. *Some brown algae.*

The *brown algae* and *red algae* are nearly all marine and include most of the seaweeds. The principal advance of these two groups over the green algae lies in the fact that the thallus shows the beginnings of cell differentiation and division of labor. The thallus is commonly divided into a rootlike or disklike *holdfast,* a *stem,* and leaflike or ribbonlike *blades.* These structures are only superficially like the roots, stems, and leaves of higher plants; the holdfast and stem of a seaweed are merely supporting structures, and the blades consist of semiindependent cells, as in other algae. Some of the brown algae (kelps) reach enormous size.

Class 2. Fungi (fŭn′ jī). The fungi are set apart from other thallophytes and from nearly all higher plants by lacking chlorophyll. Not all the various groups of fungi are closely related; in all probability, they originated at different times and from different groups of algae, so that phylogenetically the group "fungi" is not a natural one. Functionally, however, the absence of chlorophyll and the modified nutritional methods that this entails distinguish the fungi sharply from all other groups of plants.

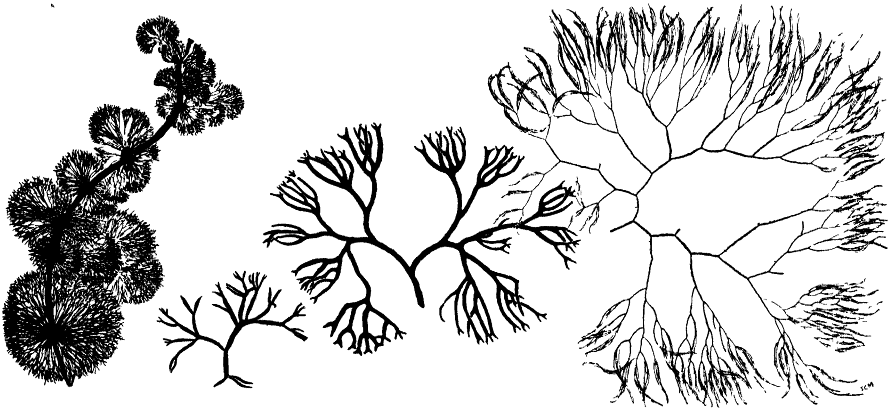

FIG. 164. *Some red algae.*

The *slime molds* (Myxomycetes, mĭx′ o mī sēt′ ēz) are among the most primitive of the thallophytes, and, although we have included them among the fungi, they are so unlike other plants that they are often given rank as a distinct phylum. In their vegetative state, they consist of a mass of protoplasm, slimelike, usually dirty white or yellowish in color, containing many nuclei but not divided into cells. This multinucleate, noncellular mass of protoplasm—often as much as a cupful in a single slime mold—shows active creeping movements. It can spread out in a thin network and, amoebalike, move about over the surface of the material on which it grows. It avoids light and seeks moisture;

rotting heaps of leaves and decaying logs are favorite habitats. A slime mold reproduces by transforming most of its mass into spores, borne on stalks; the spore masses and stalks are of various colors—brown, black, red, orange, etc. When the spores fall into water or upon moist surfaces, they germinate into small ameboid or flagellated single cells. These move about, feed, and grow; if they touch others of their kind, they fuse with them, and by such growth and amalgamation a new multinucleate slime mold is in time produced.

The *bacteria* (bak tēr′ i a) are familiar by name to all. They are single-celled plants, here classified as fungi, which probably deserve to be ranked as a separate class. Since their cells lack nuclei, like those of the blue-green algae, it is not unlikely that they have been derived from that group by loss of chlorophyll. According to the shapes of their cells, bacteria are spoken of as *cocci* (spherical), *bacilli* (rod-shaped), *spirillae* (spirals), etc. All are extremely minute.

Bacteria or their spores occur practically everywhere. We are prone to think of all bacteria as noxious, and it is true that many of them are parasites of animals and plants and that they include the causative agents of a large number of human diseases. However, the vast majority of the bacteria are not injurious, and a great many are beneficial, both from the standpoint of man and because of their indispensable roles in nature. Certain soil bacteria are responsible for much of the fertility of the soil, breaking down organic materials into a form in which they become available to the higher plants or manufacturing nitrates from the free nitrogen of the air. Without the activities of the saprophytic species, the process of decay would come to a standstill, and the world would soon be filled with dead bodies in which much of the available supply of materials necessary for life would be locked up.

A very important *symbiotic*[1] relationship should be mentioned, by means of which the plants known as *legumes* (beans, peas, vetches, and their allies) obtain a supply of nitrates. The roots of these plants are invaded by certain soil-inhabiting bacteria that cause the formation of swellings called *tubercles*, or *nodules*, within which the bacteria multiply, obtaining their food from the tissues. The bacteria have the capacity of taking nitrogen from the air and changing it into soluble nitrates, in which form it becomes available to the green plant. The relationship is thus beneficial to both organisms and enables the legumes to grow successfully on soils containing little or no available nitrogen. Other bacteria are symbionts in the intestines of herbivorous vertebrates and insects, enabling them to break down the otherwise indigestible cellulose of plants into monosaccharides.

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[1] Symbiosis is a mutually beneficial relationship between two different organisms, which may be two plants, two animals, or a plant and an animal.

The *true fungi* (Eumycetes, you′ mī sēt′ ēz) include a host of species showing the utmost diversity in form and mode of life. Among them are the yeasts, responsible for various types of fermentation, and used by man for raising bread, making beer and for other purposes. The majority of the fungi are saprophytes, but many are parasites of animals or of plants, and these are the cause of serious diseases and great economic loss.

About the same range in structural pattern occurs in the fungi as in the algae, from unicellular types, through loose cell aggregations, to types with a multicellular thallus in which the beginnings of cell differentiation and division of labor are shown. Many of the higher fungi have holdfasts and stalks comparable to those of the brown and red algae, but no fungus possesses anything that corresponds with the blades of these algae or with the leaves of higher plants. Frequently the thallus of the higher fungi forms a mass of fine, threadlike strands called *mycelia* (mī sēl′ i a); mushrooms, which we commonly think of when fungi are mentioned, are, in fact, only the fruiting bodies of a mycelial thallus, which ramifies through a mass of decaying leaves or other food source from which the mushroom appears to sprout. Peculiar modifications of the thallus occur in many parasitic fungi, related to special requirements of parasitic existence; thus in certain groups, some of the mycelial filaments form specialized organs called *haustoria* (haw stor′ i a), which can penetrate the living cells of the host and absorb water and food.

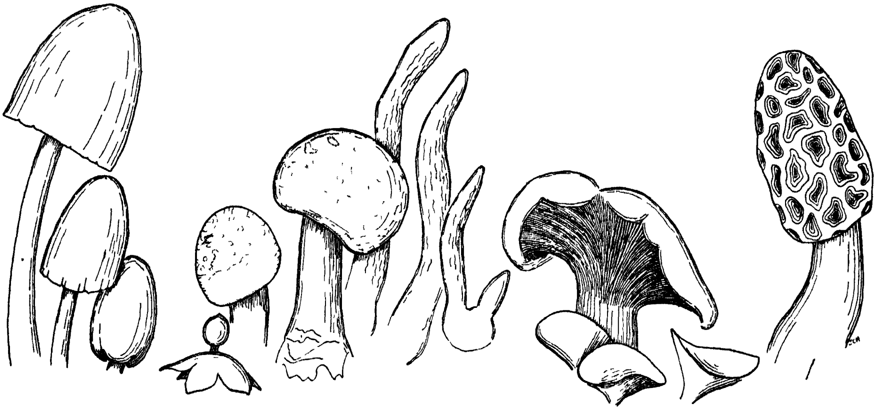

FIG. 165. *Some higher fungi (Eumycetes).*

In a large number of plants, particularly those growing in forests, the function of the root hairs has been partly or completely taken over by fungus filaments called *mycorrhiza* (mī′ kor rīz′ a); these penetrate the tissues of the root and form a mycelial mat about its surface and absorb water and dissolved substances from the soil. The relationship is evidently symbiotic, the green plant obtaining necessary substances through the agency of the fungus and the latter benefiting by having access to the foods elaborated by the green plant. Among the plants that are known to be partly or completely dependent upon mycorrhiza are many common forest trees such as oak, beech, and hornbeam, the famous heather of the Scotch Highlands, certain ferns, and nearly all orchids. In some instances, the green plant may grow in the absence of the fungus, and vice versa; this is true of certain of the forest trees and the fungi normally associated with them.[1] In other instances, the symbiotic relationship has become obligatory, neither the green plant nor the fungus being able to exist alone. This is the case in many orchids, and until this relationship was known, floriculturists had great difficulty in raising these orchids in greenhouses.

The *lichens* (lī′ kens) constitute a striking example of intimate symbiotic relations between two distantly related plants—one an alga and one a fungus—by means of which the former obtains the necessary raw materials for photosynthesis and the latter receives a supply of manufactured food. Lichens commonly form irregular patches on rocks, the bark of trees, or the soil. These patches consist of a thallus, which may be thin and tightly applied to the substratum, or rough, scaly, fibrous, leaflike, or pendulous. The color of lichens is extremely varied, but gray-greens, browns, reds, and smoky colors predominate. Each lichen consists of a single-celled green alga mingled with a mass of fungus filaments; the two plants together form the thallus. The fungus filaments absorb water and dissolved substances from the substratum; the algal cells utilize these materials for photosynthesis; and both plants make use of the manufactured food. Alga and fungus reproduce independently of each other, and the lichen association may also be propagated by joint vegetative methods. The algae and some of the species of fungi that enter into these lichen associations may live apart from each other; but many others of the fungus species that form lichens cannot survive except in partnership with an alga.

Phylum II. Bryophyta (brī of′ i ta), Greek, *bryon*, moss; *phyton*, plant.

The bryophytes (brī′ o fīts) form the second great division of the plant kingdom, the group comprising about 17,000 existing species of liverworts and mosses. They are the simplest land plants, undoubtedly derived from some group of green algae; but they differ from all thallophytes in their higher degree of structural organization, related to the requirements of life upon land, as we have already seen.

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[1] Among these fungi are many of the common forest mushrooms, such as Amanita (most of the species of which are highly poisonous), Boletus, and Russula. These mushrooms are the fruiting bodies of mycelial masses associated with tree roots.

Class 1. The Liverworts (Hepaticae, hĕ pat′ i sē) are most numerous in wet situations, such as rock or soil surfaces wet with spray or seepage. The forms with flat thalli, growing pressed against the substratum, are easily recognized; but others stand erect and have organs that resemble leaves and stems. These "leafy" liverworts can be distinguished from the mosses that they resemble by the fact that the "leaves" lack a midrib and that the spore capsule is either retained in the archegonium or, if emergent, lacks a "cap."

Class 2. The Mosses (Musci, mŭs′ ī) can live in much drier situations than liverworts but, like them, require moisture for reproduction. Their "leaves" have midribs, and the spore capsule is generally borne on a short or long stalk and has a pointed "cap" over its opening.

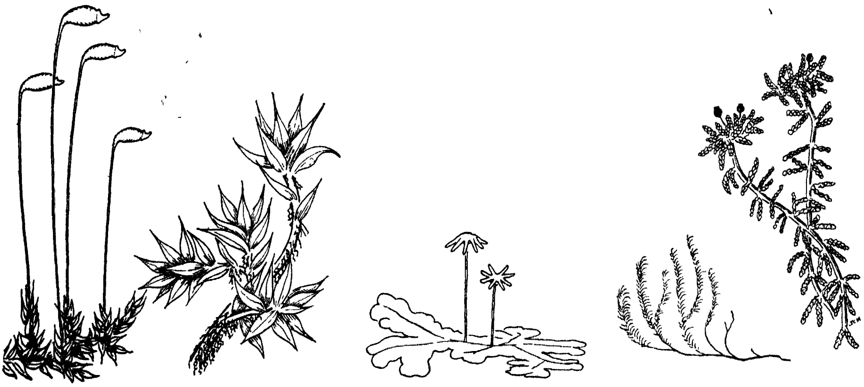

FIG. 166. *Some Bryophytes (mosses, and, in center, a liverwort).*

Phylum III. Pteridophyta (tĕr′ i dŏf′ i ta), Greek, *pteris*, fern; *phyton*, plant.

The pteridophytes (ter′ i do fīts′) constitute the third major division of the plant kingdom. Once a large and important group, they are today represented by only some 8,000 species of ferns and a small number of club mosses and horsetails. Although similar to the bryophytes in being dependent upon the presence of water films for reproduction, in all other respects, the pteridophytes are far better adapted to land life and in structural organization are closer to the spermatophytes; they are often classed with the latter as the *vascular plants*.

*Class 1. The Ancestral Pteridophytes (Psilophytales, sil lof′ ĭ tā′ lēz). This extinct class includes the oldest and simplest of the vascular plants. The earliest known fossil of the group comes from the Lower Devonian rocks of Canada; but most of our knowledge of the class is derived from the study of beautifully preserved fossils of five species found in the Middle Devonian rocks of Scotland.

The simplest of these, two species of *Rhynia and one of *Hornea, were merely erect, sparsely branched green stems, 8 to 10 inches tall, that grew thickly clustered on swampy ground. They lacked roots and leaves; the tips of some of the branches were enlarged into hollow, oval structures, in which were formed numerous asexual spores. These simple plants were evidently pteridophytes, for (1) the plant was a *free-living sporophyte* (the undiscovered gametophyte generation was probably, as in the fern, a delicate and ephemeral structure), and (2) the stem (in addition to cortical parenchyma and an epidermis that was cutinized and furnished with stomata) contained a central strand of *vascular tissue.* On the other hand, Rhynia and Hornea were more

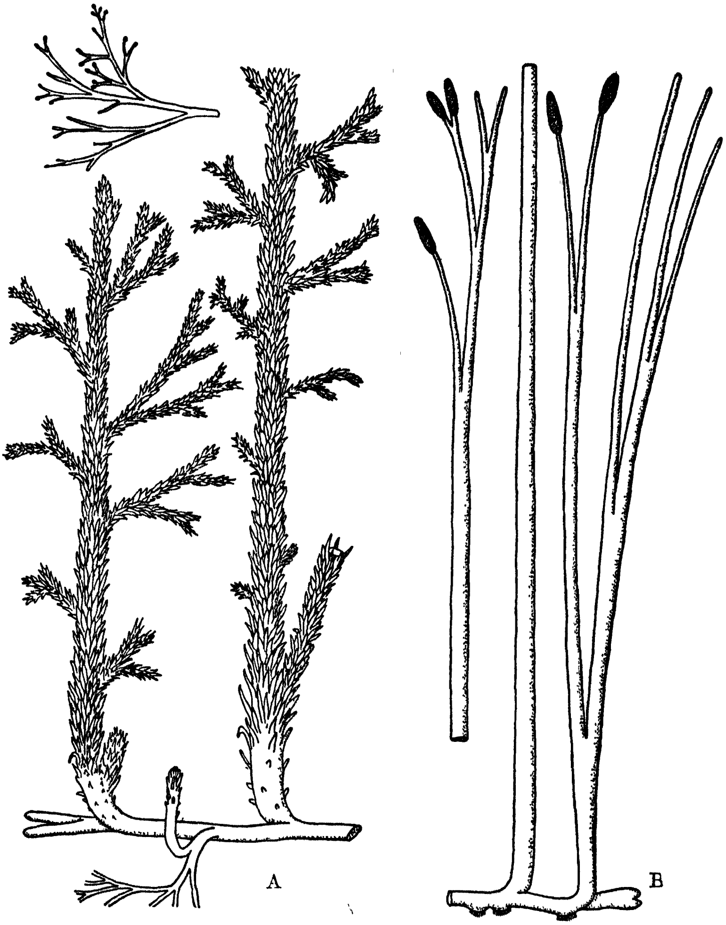

FIG. 167. *Psilophytales from the Devonian of Scotland, restored.* (*A*) *Asteroxylon mackiei;* (*B*) *Rhynia major.* (*From Haupt, An Introduction to Botany.*)

primitive than any modern pteridophyte, for (3) there were no leaves and no true roots; the stem continued under the ground as a branching rhizome that gave off rhizoids, as in the bryophytes.

Growing with Rhynia and Hornea were found more advanced members of the same group (*Asteroxylon, etc.), in which the stem had become densely covered with small scalelike or spinelike leaves; the leaves had no vascular tissue, however, and rhizoids were still the only absorptive organs. It is thought probable that the higher groups of pteridophytes developed from various Psilophytales, and that the lycopods in particular may well have been derived from plants of the Asteroxylon type.

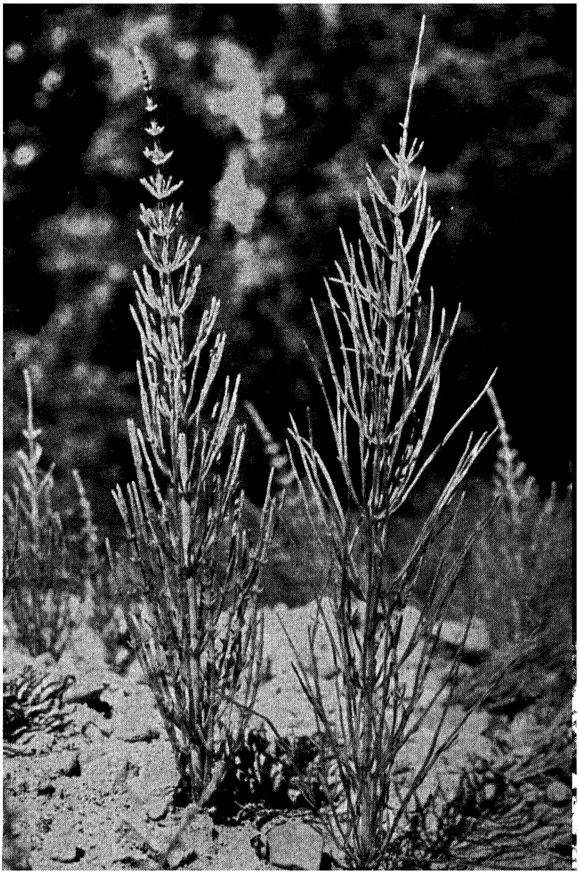

FIG. 168. *Sterile shoots of the common field horsetail* (***Equisetum arvense***), *one-half natural size.* (*From Haupt, An Introduction to Botany.*)

Class 2. The Horsetails (Equisetales, ek′ wi se tāy′ lēz). This class is represented today by the single genus Equisetum, of which there are about 30 species. Most of them are less than 18 inches tall, though in Central America and Cuba there is a giant form that grows in dense stands to a height of 40 feet, with a stem diameter of not over an inch. All the members of this genus have a subterranean rhizome (stem), from which arise the aerial stems and true roots. The aerial stems are vertically grooved and are jointed at the nodes, with a whorl of small leaves or branches at each node.

The horsetails were formerly much more important than they are today, as shown by the number and variety of fossil remains that have been found. In Paleozoic time, from the Devonian to the Permian, especially in the coal forests of the Pennsylvanian, there lived a great variety of treelike forms called *Calamites. They attained a height of 60 or even of 90 feet and a diameter of 15 inches. The stem had a thick bark and a ring of xylem enclosing a large central pith; it was abundantly branched, with a crowded tuft of leaf whorls at the apex of the main stem and at the nodes of the branches. Calamites differed chiefly from its small modern descendants in its much larger size and in the fact that the stems showed secondary thickening.

Class 3. The Club Mosses (Lycopodiales, lī′ kō pō′ dĭ ā′ lēz). These plants, like the horsetails, constitute a relict group of primitive pteridophytes. The two chief genera are Lycopodium (ground pine, running pine), with nearly 200 species, and Selaginella (little club mosses), with about 700 species, mostly tropical. Lycopodium is the more primitive; it has a sprawling stem with erect branches, all parts of the stem and branches being densely covered with small, generally sharp leaves. The spores, produced along the branches or in conelike structures at their tips, are all alike, each capable of producing a minute but generally free-living gametophyte that bears both male and female sex organs, as in most other modern pteridophytes.

Selaginella is a similar but much more delicate type of plant. It is of peculiar interest because of the fact that its reproductive processes show an advance over those of Lycopodium and the ferns and illustrate an early stage in the process of development that, in other lines of the pteridophytes, led to the differentiation of the seed plants. Instead of its spores being all alike, they are of two sorts—*microspores* and *macrospores;* and instead of the gametophytes being bisexual, the microspore produces a minute male gametophyte that remains completely enclosed by the spore wall; the macrospore germinates into a relatively much larger but still minute female gametophyte that remains within the sporangium. The microspores, with their contained male gametophytes, are shed in large numbers and in the presence of moisture liberate swimming sperms, some of which find their way to the egg cell and fertilize it. Here, then, is the beginning of the mechanism that in the spermatophytes has culminated in the production of pollen, ovules, and seeds.

The lycopods have had a long geological history. First appearing in the Devonian, they became the dominant plants of the late Paleozoic era and formed a large proportion of the trees of the coal forests. The two most important types of these lycopod trees were *Lepidodendron, the scale trees, and *Sigillaria, the seal trees. Both had large trunks, supported at the base by four to seven spreading branches that penetrated the soil and bifurcated again and again, to which were attached short true roots.

Some species of Lepidodendron (over 100 are known) had a trunk at least 114 feet tall, above which rose a crown of forking branches for a further 20 feet. In this genus, the leaves were usually only a few inches long and were borne on scalelike, diamond-shaped leaf bases attached to the trunk and branches in a regular spiral pattern. When the leaves were shed, as they were in all the older parts of the tree, the leaf bases remained attached to the bark, their pattern suggesting the arrangement of scales on a fish. The spore-bearing organs were conelike structures at the tips of the branches; like Selaginella, the scale and seal trees produced micro- and macrospores. The microspores were shed in such vast amounts that they make up a considerable part of the material from which coal was formed.

Sigillaria agreed with Lepidodendron in most respects, but its trunk was generally unbranched and rose to a height of from 70 to nearly 100 feet in certain species. At the top, for about 10 feet, the trees were clothed with erect, rigid, grasslike leaves, generally like those of Lepidodendron but sometimes much larger. The leaf bases were usually arranged in vertical rows instead of in spirals, and the name *seal tree* was suggested by their hexagonal shape.

Class 4. The Ferns (Filicales, fĭl′ i kā′ lēz). The ferns, comprising some 8,000 living species, include the great majority of modern pteridophytes. They are widely distributed but are most at home in the tropics; they prefer moist, shady habitats, although some species such as the bracken fern may grow in very dry situations. Ferns attain their greatest size in the tropics, where certain species are trees that attain a height of 50 to 80 feet. The stems of such tree ferns are erect, woody, and unbranched, often covered with persistent leaf bases, and have a cluster of large compound leaves at the apex. Most ferns, however, have a horizontal or short erect underground stem (a rhizome), from which the leaves rise singly or in clumps.

Phylum IV. Spermatophyta (sperm′ a tŏf′ i ta), Greek, *sperma*, seed; *phyton*, plant.

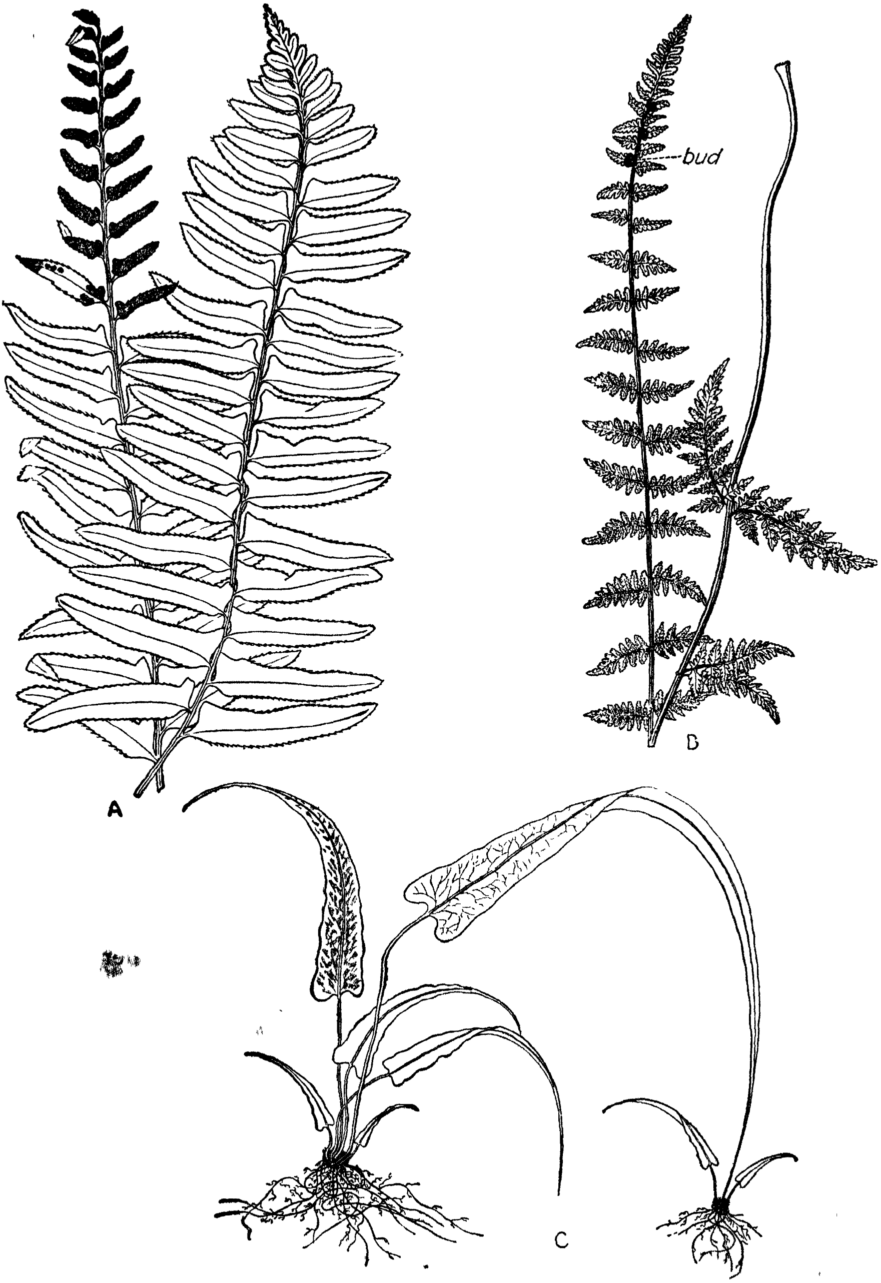

Fig. 169. *Common ferns. (A) Christmas fern (Polystichum); (B) bladder fern (Cystopteris), showing reproductive buds; (C) walking fern (Camptosaurus), showing vegetative multiplication. (From Miller and Blaydes, Methods and Materials for Teaching Biological Sciences.)*

The spermatophytes (sperm′ ă to fīts), or seed plants, not only are the most highly organized of plants but also are the dominant phylum. There are some 133,500 species known in this group, which includes most of the familiar trees, shrubs, and vines and nearly all the plants economically important to man. We have already described in some detail the structure and functioning of a member of this group, and here we need only to mention the principal subdivisions so far as they represent modifications of the basic design.

Class 1. The Gymnosperms (jim′ no sperms) form the first subdivision of the spermatophytes. The plants of this group are distinguished from the other seed plants chiefly by a difference in their reproductive mechanism. The name means "naked seed" and refers to the fact that there are no flowers with ovaries in which the seeds are enclosed, but instead the seeds are borne on the inner faces of scalelike leaves, which are generally arranged spirally on an axis so as to form a structure called a *cone*. The group includes the modern pines, spruces, firs, junipers,[1] sequoias, gingkoes, and cyads[2] and various extinct groups. Structurally, the gymnosperms do not differ greatly from the flowering plants. The wood generally contains resin or mucilage ducts; and in the pines and their allies, the xylem is composed only of tracheids, without tracheal vessels, and the phloem does not contain companion cells. All the members of this group are woody in structure.

*Subclass 1. The Seed Ferns (Cycadofilicales, sī′ kad o fil′ i ka′ lēz) are an extinct group that was common in the late Paleozoic. They had all the appearance of true ferns and were originally classified in that group; but later it was discovered that they produced pollen and seeds and that they must therefore be regarded as primitive spermatophytes. The plants were dioecious; the pollen and ovules were borne on only slightly modified leaves and never in cones; the seeds hung from the tips or midribs of the leaves. Some of the members of this group had the aspect of tree ferns, others were vines, and still others were herbaceous. The cycads are thought to have been derived from Cycadofilicales.

Subclass 2. The Cycads (Cycadales, sī′ kad ā′ lēz) were an important group during the Mesozoic era but are represented today by only 9 genera and about 90 species. The plants are like palms or tree ferns in appearance, with a thick columnar stem that rarely branches and is often covered by an armor of dead leaf bases, and with a crown of large feathery leaves. The cycads are dioecious, producing male and female cones. An interesting feature, shared by cycads with the gingkoes and doubtless with the extinct seed ferns, is the fact that the sperms developed in the pollen tube are ciliated and are able to swim, like those of the bryophytes and pteridophytes. In the two latter groups, motile sperms are necessary because of the method of fertilization; but in plants that have a pollen tube, this feature can only represent a survival of ancestral characteristics. The presence of motile sperms and the leaflike structure of the cone scales in some cycads indicate that the members of this group are the most primitive of existing seed plants.

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[1] In the junipers and yews, the cone is often berrylike.

[2] Cycads are today mostly tropical; the "coontie," or Florida arrowroot, is an example of this group.

Cycads are characteristically very slow-growing and long-lived plants, and individuals of some of them certainly reach an age of upward of one thousand years—probably much more. The modern representatives of the group are practically confined to tropical and subtropical regions, although during the Mesozoic, cycads were widely distributed. A familiar member of the group is the "coontie," or Florida arrowroot, which has a subterranean stem and a crown of leaves growing apparently from the ground. A larger species (*Cycas revoluta*) has been introduced and is cultivated in Florida as an ornamental.

Subclass 3. The Maidenhair Trees (Ginkgoales, ging′ ko ā′ lēz) are an ancient group, of which today there is a single survivor. The maidenhair tree, almost unknown in the wild state, though extensively cultivated, grows to a height of 90 feet. It is freely branched and bears flattened, generally bilobed leaves that resemble those of the maidenhair fern. Male and female cones are borne on separate trees; they are small and inconspicuous. Members of this group are known as early as the Carboniferous, and the genus Ginkgo, to which the maidenhair tree belongs, had its origin as early as Triassic time.

Subclass 4. The Large-leaved Evergreen Trees (Cordaitales, kor′ dāī-tā′ lēz) were the dominant gymnosperms of the late Paleozoic. They were trees, sometimes as much as 120 feet tall and 3 feet in diameter at the base; in the larger ones, the lower two-thirds or three-fourths of the trunk was unbranched; the upper third or quarter had a dense crown of branches bearing many large, simple leaves. In one genus, *Cordaites, the leaves sometimes reached a length of 6 feet and a width of 6 inches. In other genera, the leaves were smaller, sometimes strap-shaped, with blunt or sharp tips, sometimes grasslike, with a length of 20 inches and a width of ½ inch. The leaves were thick and had parallel veins. There were separate male and female catkinlike cones borne on the same tree; the female cones generally matured only a single seed with a hard seed coat and fleshy rind. The wood of the trunk was much like that of the modern pines, but there was a large central pith. Members of this group showed a combination of the characteristics of seed ferns, cycads, gingkoes, and conifers; they are thought to have been most closely allied to the two latter groups.

Subclass 5. The Conifers (Coniferales, ko nĭ′ fer ā′ lēz). The needle-leaved evergreen trees constitute by far the most conspicuous group of living gymnosperms. This is true whether one considers number of individuals, number of genera (46) and species (nearly 500), size of individuals (many are large, some—the sequoias—the most gigantic of living things, with trunks almost 400 feet tall), or economic importance. (They provide the softwoods of the lumbering industry, pulpwood for paper mills, resin, and turpentine.) The group includes the Auracarian pines,[1] the sequoias (California "big trees"),[2] and the pines, spruces,

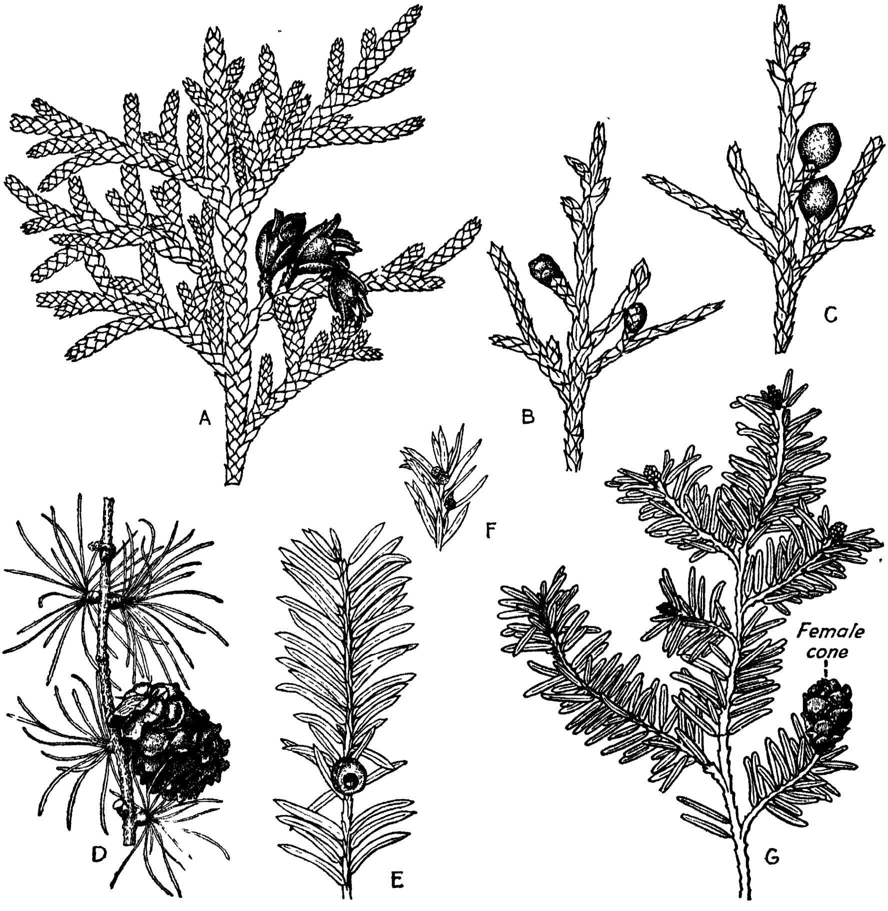

FIG. 170. *Some representative conifers (Gymnosperms). (A) Arborvitae; (B) red cedar with male cones; (C) red cedar with female cones (juniper "berries"); (D) tamarack; (E) yew with female cones; (F) yew with male cones; (G) hemlock. (From Miller and Blaydes, Methods and Materials for Teaching Biological Sciences.)*

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[1] Now confined to the Southern Hemisphere but formerly more widespread.

[2] Closely related but smaller forms can be traced back to the Permian.

firs, junipers, or "red cedars," larches, or "tamaracks," cypresses, and yews. In the conifers, pollen is produced in small male cones and is broadcast on the wind in enormous amounts, reaching the female cones by accident. The leaves are needlelike or scalelike, and the wood lacks vessels and generally possesses resin ducts.

Class 2. The Angiosperms (an′ jĭ o sperms) are the flowering plants. The name means "covered seed" and refers to the fact that the seeds develop inside a closed ovary. The group includes about 133,000 species, many of which are herbaceous, others of which are woody. The xylem of all angiosperms contains vessels in addition to tracheids, and the phloem has companion cells. The groups includes most of the plants important to man as sources of food, clothing, and industrial materials. Members of the group are often referred to as the "broad-leaved plants." Gymnosperms and angiosperms agree in producing seeds, as opposed to the three lower phyla. The angiosperms differ from the gymnosperms, however, in the following respects: (1) the presence of *vessels in the xylem;* (2) the production of *flowers* and *fruit;* (3) the formation of a *pistil,* to the apex of which pollen adheres and through which the pollen tube must grow to reach the ovule;[1] (4) the predominance of *insect pollination* (though wind pollination also occurs in several large groups); and (5) *the further reduction of the gametophyte* to merely a few cells existing but a few days.

The angiosperms include some 300 families of plants, but these can be grouped into two main subdivisions—*monocotyledons* and *dicotyledons.* The principal distinctions between these two groups are as follows:

1. The leaves of monocotyledons are generally parallel-veined and almost always have smooth, even margins, whereas the leaves of dicotyledons are generally net-veined and are very often toothed, lobed, or divided.

2. The flowers of the monocotyledons are generally built on a plan of three, *i.e.*, the number of flower parts of any one kind (petals, sepals, etc.) is three or some multiple of three; in the dicotyledons the number of parts of each kind is generally four or five or some multiple of four or five.

3. In the stems of the monocotyledons, the conducting tissue is in numerous vascular bundles scattered through the stem but not arranged n a single ring; in dicotyledonous stems, the conducting or vascular tissue either is a hollow cylinder surrounding the pith and increasing in width as the stem grows older or is distributed in separate bundles arranged in a single circle.

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[1] In the gymnosperms, the wind-borne pollen falls into the angles between the cone scales and is thence drawn up through the neck of the ovule by a sticky secretion first extruded from the ovule and then resorbed; the pollen tube has merely to penetrate the inner layer of ovule tissues and is very short.

4. The embryos of the seeds of monocotyledons have only one cotyledon or seed leaf, whereas in the dicotyledons, the embryos generally have two cotyledons.

Subclass 1. The Monocotyledons (Monocotyledones, mon′ o cot′ i lēd′ o nēz) number approximately 27,000 described species. Only four of the most important families can be mentioned here.

The Gramineae (grass family) includes a number of species that are of preeminent economic importance. In the tropics, bamboo is one of the most valuable of plants, being used for a great variety of purposes. In the temperate regions, hay and forage for cattle are provided chiefly by small grasses. Sugar cane is one of the two chief sources of sugar (the other being the sugar beet, a dicotyledon). Most important of the grasses are the cereals—wheat, corn, oats, rice, rye, and barley. All members of the grass family are wind-pollinated.

The Palmaceae (palm family) is chiefly tropical; the appearance of its members is familiar to all. In this group, a large number of simple flowers develop within a single leaflike bract. The coconut palm, date palm, sago palm, and others are put to a variety of uses by inhabitants of the tropical and subtropical regions.

The Liliaceae (lily family) includes some of the most typical and easily recognized of monocotyledons. Here the floral parts are separate and occur in threes or in multiples of three, with the petals generally brightly colored, and often the sepals as well. The plant is generally herbaceous and is usually provided with a bulb or some other form of underground stem. Asparagus, onion, trillium, lily-of-the-valley, true lilies, tulip, and dogtooth violet are members of this family.

The Orchidaceae (orchid family) is the most advanced and specialized of all the families of monocotyledons and is largest in number of species, though not to be compared with the Gramineae in number of individuals. The flowers of orchids are highly modified in relation to various special arrangements for pollination by particular kinds of insects or by hummingbirds. Aside from their value as ornamental plants, orchids are of little economic importance; the only one that plays a part in ordinary commerce is a Mexican species from which vanilla is obtained.

Subclass 2. The Dicotyledons (Dicotyledones, di′ cot y lēd′ o nēz), with approximately 106,000 known species, constitute a much larger assemblage than the monocotyledons. Two great divisions may be distinguished within the subclass, based upon the characteristics of the flower. In Division I, the petals are either present and distinct from one another (Polypetalae) or absent (Apetalae); in Division II (Sympetalae), the petals are partly or completely fused into a tube that surrounds the stamens and pistils. These two divisions are also characterized by numerous other differences.

Division I. Among the important groups belonging to this assemblage are several small families with wind-pollinated, inconspicuous flowers; these include some of our most common deciduous or hardwood trees—oaks, hickories, pecans, elms, walnuts, chestnuts, willows, birches, beeches, and poplars.

The Ranunculaceae (buttercup family) includes herbs that have five petals, numerous stamens and numerous separate pistils; it includes such well-known plants as clematis, anemone, hepatica, marsh marigold, peony, larkspur, and columbine. In many of the cultivated species, so-called "double" flowers have been produced by transformation of stamens and pistils into petals.

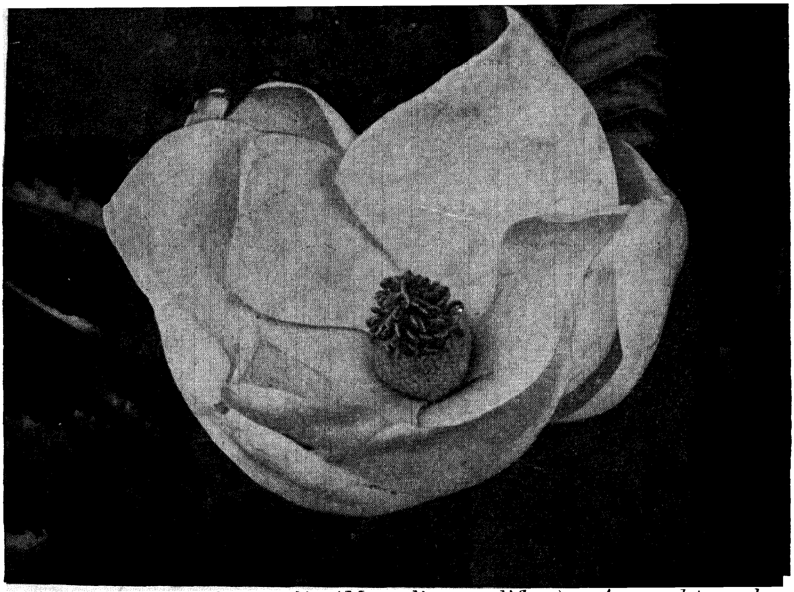

FIG. 171. *The flower of magnolia (Magnolia grandiflora) A complete and regular dicotyledonous flower, its numerous stamens and carpels borne in spiral arrangement on an elongated receptacle. One-half natural size. (From Haupt, An Introduction to Botany.)*

The Cruciferae (mustard family) includes plants with a pungent taste and with four sepals, four petals in a single circle, four long and two short stamens, and two pistils. Included in this family are stock, water cress, horse-radish, mustard, cabbage, turnip, and radish.

The Rosaceae (rose family) includes many useful as well as beautiful plants, among which are roses, strawberries, raspberries, blackberries, peaches, apricots, plums, cherries, apples, pears, and quinces.

The largest of the families of Division I is the Leguminosae (legumes), characterized by its irregular flowers (which are highly adapted, like those of orchids, to insect pollination) and by the ripening of the ovary into the well-known "pod." The legumes include such plants as sweet pea, wisteria, lupine, sensitive plant, locust, honey locust, coffee tree, clover, alfalfa, Crotalaria, beans and peas, peanuts, and acacias, as well as many tropical trees.

The most advanced family of the division is the Umbelliferae, in which the flowers form characteristic flat-topped clusters; examples are carrot, celery, and parsnip.

Other well-known plants belonging to the first division of the dicotyledons but not included in any of the preceding families are tulip tree, magnolia, bay, basswood, sycamore, maple, ash, buckeye, horse chestnut, box elder, sweet gum, black gum, violets, pinks, geranium, nasturtium, fuchsia, cotton, flax, hemp, currants, gooseberries, grapes, citrus fruits, tea, and cacao.

Division II. The plants of this assemblage, with tubular corollas, include the highest dicotyledonous families, only a few of which can be mentioned here.

The Ericaceae (heath family) is characterized by having two sets of five stamens each, so that there are five circles of flower parts. The members of this family are mostly shrubs; included in it are trailing arbutus, bearberry, heather, rhododendron, azalea, mountain laurel, wintergreen, huckleberries, blueberries, and cranberries.

The Labiatae (mint family) can be recognized by the two-lipped corolla, square stems, opposite leaves, and four-lobed ovary. It includes many strongly scented plants, among which are pennyroyal, lavender, mint, horehound, savory, marjoram, thyme, sage, rosemary (but not the "rosemary" of the Florida scrub), and catnip.

The Solanaceae (nightshade family) includes plants with conspicuous, regular corollas and with floral parts arranged in four circles. Here are included nightshade, red pepper, ground cherry, belladonna, Jimson weed, Irish potato, tomato, and tobacco.

The highest of the families of Division II is the Compositae (composites), characterized by having numerous small flowers compacted into a head that looks like a single large flower. The composites are mostly herbaceous plants, abundant in the temperate regions. Among the better known members of this family are dandelion, sunflower, goldenrod, thistle, beggar ticks, blazing star, daisies, asters, everlasting, ragweed, cockle burr, zinnia, dahlia, cosmos, marigold, chrysanthemum, sagebrush, burdock, and lettuce. The family is noteworthy for the number of noxious weeds that it includes.

Other well-known dicotyledons with tubular flowers that do not belong to any of the preceding families are the coffee plant, cinchona (from which quinine is obtained), sweet potato or yam, olive, and the gourd fruits (watermelon, muskmelon, cucumber, pumpkin, squash).

THE ANIMAL KINGDOM

In our treatment of the varied patterns of animal life, under the topic of the structure and functioning of the individual organism (Chap. XV), we were not concerned with classification as such but merely with demonstrating the ability of animals to meet their common functional requirements by a variety of structural patterns. It was sufficient for that purpose to group animals under only four divisions—Protozoa, simple Metazoa at the cellular level, intermediate Metazoa at the tissue level, and complex Metazoa at the organ-system level of construction, but this could be done only by ignoring many important differences in structure. When these are taken into consideration, it becomes necessary to recognize at least 11 animal phyla. Authorities do not agree as to just how many phyla may be distinguished; but they do agree that the following are of major importance: Protozoa, Porifera, Coelenterata, Ctenophora, Platyhelminthes, Nemathelminthes, Mollusca, Echinodermata, Annelida, Arthropoda, and Chordata. These 11 sharply distinguished phyla contain by far the greater number of all animals. There are, in addition, a number of groups of minor importance, some of which are clearly of phylum rank, others, of uncertain status; those that will require brief mention are the Nemertinea, Rotifera, Bryozoa, and Brachiopoda.

Characteristics Used in Classifying Animals. The phyla are distinguished from one another not so much by the possession of unique characteristics as by unique combinations of characters. Among the important features in which they may differ are the following:

1. *Degree of Cell Differentiation.* Animals are either (*a*) unicellular (or composed of a relatively small number of undifferentiated cells) or (*b*) composed of many cells exhibiting various degrees of differentiation and division of labor. Those of the first category are the Protozoa; those of the second, the Metazoa.

2. *Number of Germ Layers.* Metazoa develop either two or three germ layers (embryonic cell layers). Those with two germ layers are said to be *diploblastic;* those with three germ layers are *triploblastic.* The three layers are, beginning with the outermost, *ectoderm, mesoderm,* and *entoderm.* Mesoderm is lacking in diploblastic animals.

3. *Kinds of Symmetry.* Although a few animals are asymmetrical, possessing no plane of symmetry, the great majority are built on a symmetrical plan, with spherical, radial, or bilateral arrangement of body

parts. *Spherical symmetry* is that of a ball, any section through the center dividing the organism into symmetrical or mirrored halves. *Radial symmetry* is that of a wheel or cylinder, any one of several sections through the main axis dividing the organism into symmetrical halves. *Bilateral symmetry* is that of a boat or wagon, there being only one section, a vertical one that passes through the longitudinal axis, that will divide the organism into mirrored halves.[1]

4. *Metamerism.* Several phyla are characterized by the fact that their members have bodies composed of linear series of segments, each segment being built on the same basic structural plan and repeating, in more or less modified form, the structure of the segments anterior and posterior to it. This condition is known as *metamerism,* and each segment is a *metamere* (or *somite*).

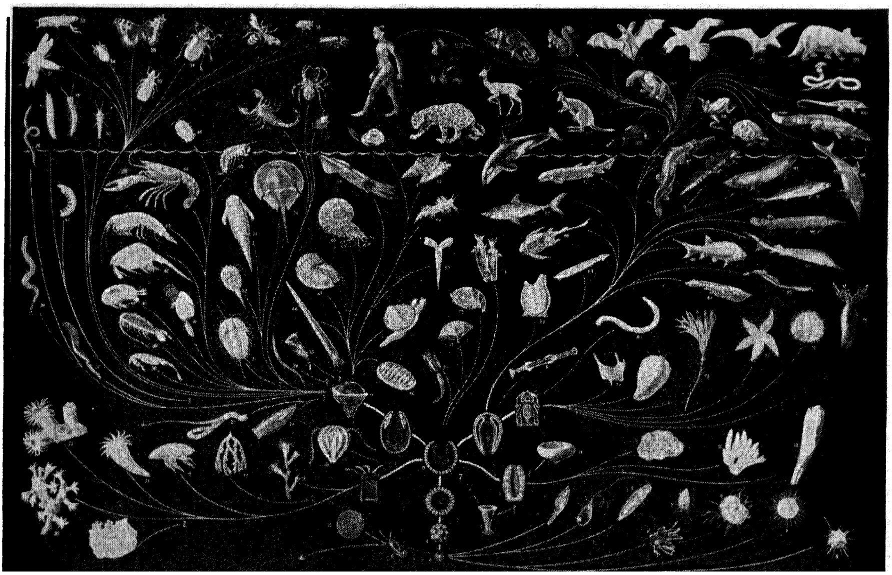

FIG. 172. *A phylogenetic diagram of the Animal Kingdom, including some of the important fossil groups. (Courtesy of Ward's Natural Science Establishment.)*

5. *Body Cavities or Internal Spaces.* Any metazoan has either one or two body cavities. In the *lower Metazoa,* the body is saclike in general

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[1] Just as there may be minor departures from complete bilateral symmetry in a boat or wagon, bilaterally symmetrical animals may show imperfect symmetry in details of their structure. Thus in man the intestine, though essentially a bilaterally symmetrical structure, is so long that it is assymetrically coiled in the abdomen; and the originally symmetrically paired aortic arches have been reduced in number to a single unpaired arch that lies on the left side of the median line of the body.

plan, *i.e.*, the two-layered body wall surrounds a single large space that has but one opening. The cavity may be a true digestive cavity and the single opening a mouth (as in the Coelenterata), or it may be a cloaca or water cavity and the single opening an excurrent pore (as in the Porifera). In the *higher Metazoa*, the body is constructed according to the tube-within-tube plan. The alimentary canal is a tube open at both ends (mouth and anus), lined with digestive cells (entoderm). In addition, a new cavity lined with mesoderm separates the body wall from the digestive tube; this is the coelom.

6. *Special Features and Combinations of Features.* A number of phyla and certain subphyla are characterized by the possession of structures that are not found in any other group. Among examples that might be cited are the pores and canal system of the Porifera, the stinging cells (nematocysts) of the Coelenterata, the water-vascular system of the Echinodermata, the hollow dorsal nervous system and notochord of the Chordata, and the vertebral column of the subphylum Vertebrata.

Even when structures are shared by more than one phylum (for instance, metamerism by Annelida, Arthropoda, and Chordata; a ventral ladderlike nervous system by Annelida and Arthropoda), they occur in combinations that are distinctive and diagnostic of each phylum. Thus the combination of metamerism, ventral ladderlike nervous system, soft skin, and unsegmented appendages, with other features, is peculiar to the Annelida. In the Arthropoda, the first two characteristics are combined with the presence of an exoskeleton and jointed appendages. In the Chordata, metamerism occurs in combination with a hollow dorsal nervous system, notochord, and other peculiar features.

7. *Habitat.* The environment in which an animal lives is *not* a criterion for its classification; but information concerning the major habitat or habitats of the members of a phylum aids in forming a conception of the group. Thus all the Echinodermata are inhabitants of the ocean; the greater number of the Platyhelminthes and at least half of the Nemathelminthes are parasitic; and very few of the Porifera occur in fresh water, though all are aquatic.

In the accompanying table of the chief groups of animals and in the discussion of them that follows, extinct groups are starred.

The Animal Phyla and Some of Their Subdivisions

Subkingdom I. Protozoa. The unicellular animals.

Phylum I. PROTOZOA. Animals composed of a single cell or of a colony of similar cells.

Subkingdom II. Metazoa. The multicellular animals, with specialized tissues.

Metazoa without a true digestive cavity.

Phylum II. PORIFERA. The Sponges. Diploblastic.

Metazoa with a true digestive cavity. Digestive cavity the only cavity in the body, with mouth but no anus.

Phylum III. COELENTERATA. The Coelenterates: Hydra, corals, jellyfishes, sea anemones, etc. Diploblastic.

Phylum IV. CTENOPHORA. The Comb Jellies or Sea Walnuts. Transitional between diplo- and triploblastic. All the remaining phyla triploblastic.

Phylum V. PLATYHELMINTHES. The Flatworms: Planaria, liver flukes, tapeworms, etc.

Coelom present in addition to digestive cavity; body constructed on tube-within-tube plan, with mouth and anus both present. Body not segmented (nonmetameric).

Phylum VI. NEMATHELMINTHES. The Roundworms.

Phylum VII. ECHINODERMATA. The Echinoderms. Radially symmetrical.

- Class 1. The Starfishes (Asteroidea).
- Class 2. The Serpent Stars or Brittle Stars (Ophiuroidea).
- Class 3. The Sea Urchins and Sand Dollars (Echinoidea).
- Class 4. The Sea Cucumbers (Holothuroidea).
- Class 5. The Sea Lilies or Feather Stars (Crinoidea).

Phylum VIII. MOLLUSCA. The Mollusks. Bilaterally symmetrical or twisted.

- Class 1. The Chitons (Amphineura).
- Class 2. The Snails (Gastropoda).
- Class 3. The Tooth Shells (Scaphopoda).
- Class 4. The Bivalve Mollusks: clams, etc. (Pelecypoda or Lamellibranchiata).
- Class 5. The Cephalopod Mollusks: squids, etc. (Cephalopoda).

Body segmented (metameric).

Phylum IX. ANNELIDA. The Segmented Worms: earthworms, leeches, etc.

Phylum X. ARTHROPODA. The Arthropods.

- Class 1. The Crustaceans (Crustacea): crayfishes, crabs, shrimps, *trilobites, etc.
- Class 2. The Arachnids (Arachnida): spiders, mites, scorpions, king crabs, *eurypterids, etc.
- Class 3. The Onychophora (Onychophora): Peripatus, wormlike, with many legs, nephridia as in Annelida and tracheae as in myriapods and insects.
- Class 4. The Myriapods (Myriapoda): centipedes, millipedes, etc.
- Class 5. The Insects (Insecta): grasshoppers, dragonflies, bugs, beetles, flies, butterflies and moths, bees and wasps, etc.

Phylum XI. CHORDATA. The Chordates; with notochord, dorsal hollow nerve cord, and gill slits in pharynx.
- Subphylum *A*. The Primitive Chordates (Protochordata): acorn worms, sea squirts or tunicates, and Amphioxus.
- Subphylum *B*. The Vertebrates (Vertebrata or Craniata).
  - *Class 1. The Ostracoderms (Ostracodermata): Primitive jawless vertebrates of the early Paleozoic, ancestral to the higher forms.
  - Class 2. The Lampreys and Hagfishes (Cyclostomata).
  - Class 3. The Sharks and Rays (Elasmobranchii).
  - Class 4. The True or Bony Fishes (Pisces), including the lungfishes, *lobe-finned fishes, and ray-finned fishes.
  - Class 5. The Amphibians (Amphibia): The late Paleozoic *stegocephalians and the modern salamanders, frogs and toads, and blindworms.
  - Class 6. The Reptiles (Reptilia): The extinct *cotylosaurs, *ichthyosaurs, *plesiosaurs, and *archosaurs and the modern turtles, crocodilians, tuatara, lizards, and snakes.
  - Class 7. The Birds (Aves): The extinct *reptilian birds and the true birds. Warm-blooded; feathered.
  - Class 8. The Mammals (Mammalia). Warm-blooded; hairy.
    - Subclass 1. The egg-laying mammals (Prototheria or Monotremata).
    - Subclass 2. The marsupial mammals (Metatheria or Didelphia).
    - Subclass 3. The placental mammals (Eutheria or Monadelphia).
      - Superorder 1. The Insectivore Stock:
        - Order 1. The insectivores (Insectivora): moles, shrews, etc.
        - Order 2. The "flying lemurs" (Dermoptera).
        - Order 3. The bats (Chiroptera).
        - Order 4. The primates (Primates).
          - Suborder 1. The lemurs (Lemuroidea).
          - Suborder 2. The tarsioids (Tarsioidea).
          - Suborder 3. The anthropoid primates (Anthropoidea).
            - Series 1. The New World monkeys (Platyrhini).
              - Family 1. The marmosets (Callitrichidae).
              - Family 2. The capuchins, etc. (Cebidae).
            - Series 2. The Catarrhini (Catarrhini).
              - Family 1. The Old World monkeys, baboons, etc. (Cercopithecidae).
              - Family 2. The manlike or "anthropoid" apes (Simiidae).
              - Family 3. Ancient and modern men (Hominidae).
                - *Genus 1. Peking man (Sinanthropus).
                - *Genus 2. Java man (Pithecanthropus).
                - *Genus 3. Piltdown man (Eoanthropus).
                - Genus 4. True man (Homo).

*1. Heidelberg man (*Homo heidelbergensis*).
*2. Neanderthal man (*Homo neanderthalensis*).
*3. Rhodesian man (*Homo rhodesiensis*).
4. Modern man (*Homo sapiens*).

Superorder 2. The Rodent Stock: The rodents (Rodentia).

Superorder 3. The Edentate Stock:
- Order 1. The ant bears and sloths (Edentata).
- Order 2. The scaly anteaters (Pholidota).
- Order 3. The aardvarks (Tubulidentata).

Superorder 4. The Carnivore Stock:
- Order 1. The carnivores (Carnivora).
  - *Suborder 1. The creodonts (Creodontia): primitive Eocene carnivores.
  - Suborder 2. The fissipedes (Fissipedia): terrestrial carnivores; cats, hyenas, dogs, raccoons, weasels, bears, etc.
  - Suborder 3. The seals and walruses (Pinnipedia).

Superorder 5. The Whales and Dolphins (order Cetacea); probably derived from creodonts, in spite of blood-test indications of relationship to pigs.

Superorder 6. The Ungulates or Hoofed Mammals.

*Archaic ungulate orders of the Eocene, small-brained and slow-footed—taligrades (example, Pantolambda), condylarths (example, Phenacodus), amblypods (examples, Coryphodon, the uintatheres).

Modernized Ungulates

- Order 1. The odd-toed ungulates (Perissodactyla).
  - Family 1. The horses (Equidae).
    - *Genus 1. Eohippus, Eocene.
    - *Genus 2. Mesohippus, Oligocene.
    - *Genus 3. Merychippus, Miocene.
    - *Genus 4. Pliohippus, Pliocene.
    - Genus 5. Equus, Pleistocene and Recent; all modern horses, asses, zebras.
  - Family 2. The tapirs (Tapiridae).
  - Family 3. The rhinoceroses (Rhinocerotidae).
  - *Family 4. The chalicotheres or clawed ungulates (Chalicotheriidae).[1]
  - *Family 5. The titanotheres (Titanotheriidae).[2]
- Order 2. The even-toed ungulates (Artiodactyla).
  - Suborder 1. Swinelike ungulates (Suina).
    - Family 1. The hippopotamuses (Hippopotamidae).

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[1] Often placed in a separate order, the Ancylopoda.

[2] Often treated as a separate order, the Titanotheria.

*Family 2. The "giant pigs" (Entelodontidae).
Family 3. The pigs or swine (Suidae).
Family 4. The peccaries (Tayassuidae).
Suborder 2. The ruminants (Ruminantia).
Series *A*. The mouse deer (Tragulina).
Series *B*. The camels and llamas (Tylopoda).
*Series *C*. The oreodonts (Oreodontia).
Series *D*. The deerlike ruminants (Pecora).
Family 1. The deer (Cervidae): deer, moose, elk, reindeer, etc.
Family 2. The giraffes (Giraffidae).
Family 3. The cattle family (Bovidae): oxen, bison, yak, sheep, goats, ibexes, gnus, antelopes, etc.

Subungulates

Order 3. The coneys (Hyracoidea).
*Order 4. The South American ungulates (Noto-ungulata): Strange forms—toxodonts, litopternes, etc.
Order 5. The elephants and mastodons (Proboscidia).
a. *Ancestral forms: Moeritherium, Paleomastodon, Phiomia.
b. *The deinotheres.
c. *The mastodon series.
d. The elephant series: *Stegodon, the elephants (Elephas and Loxodonta) and *mammoths.
Order 5. The dugongs and manatees (Sirenia).

Phylum I. Protozoa (pro′ to zo′ a), Greek *protos*, first; *zoön*, animal. Single-celled animals or colonies of relatively loosely aggregated cells exhibiting little or no cell differentiation or division of labor, though some colonies, like Volvox, have differentiated germ cells. Minute, mainly microscopic forms. Examples: Amoeba, Euglena, Volvox, Paramecium, Stentor, etc.[1]

Every zoologist recognizes the Protozoa as the simplest of all animals. Because of their microscopic size, they do not come within our everyday experience, and one who for the first time sees them swarming in a drop of pond water under the microscope feels as though he were discovering a new world. Protozoa are unable to live under permanently dry conditions, but they may occur in fabulous numbers in moist or aquatic situations. Fresh-water ponds, lakes, and streams have many of them; uncountable numbers live in the sea; and moist soil supports a great population of them. Many species of Protozoa are parasitic, living on or within the bodies of other animals. Among the more interesting and important members of the latter group are the parasitic species that live within the red blood cells of man and produce malaria.

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[1] Euglena, Volvox, and Stentor may also be regarded as Algae, since they contain chlorophyll; but since they possess a number of animal characteristics, they are also included among the Protozoa by zoologists. They are excellent examples of the Protista.

Approximately 15,000 species of Protozoa have been described.

Phylum II. Porifera (po rĭf′ er a), Latin, *porus*, pore; *ferre*, to bear.

The sponges. Primitive aquatic Metazoa, mostly marine and invariably sessile; usually colonial or consisting of many individuals indistinguishably fused; exhibiting the following characters:

Body wall diploblastic, consisting in the adult of an outer dermal epithelium and an enclosed gastral epithelium, between which there is usually a noncellular layer, the mesoglea. The mesoglea is a jellylike substance, in which occur the germ cells and a skeleton of spicules or spongin. Embryological data indicate that the two germ layers are not homologous with the ectoderm and entoderm of higher phyla. Symmetry radial or lacking. No metamerism. Possessed of a generalized body cavity, the cloaca, reached from the outside by way of many small incurrent pores and opening to the outside by a single large excurrent pore, the osculum. Body cavity not homologous with that of the coelenterates, which it superficially resembles.

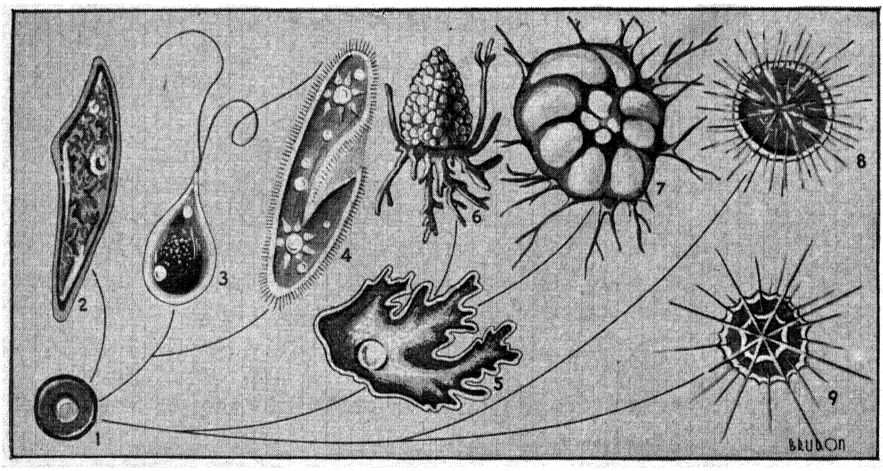

FIG. 173. *Some Protozoa.* (1) *Hypothetical ancestral cell;* (2) *sporozoan;* (3) *flagellate;* (4) *ciliate* (*Paramecium*); (5) *rhizopod* (*Amoeba*); (6) *shelled rhizopod* (*Difflugia*); (7) *foraminiferan;* (8) *heliozoan;* (9) *radiolarian.*

Among the features peculiar to this group are the presence of pores in the body wall, forming part of a canal system, and the presence in the gastral epithelium of collared cells, the flagella of which create a current of water through the canals that brings in food particles and oxygen and carries away waste products.

Sponges are an aberrant group that belongs near the bottom of the animal series and outside the main line of metazoan evolution; hence they are often separated from the rest of the Metazoa and are called Parazoa. A very few species of sponges live in fresh water. The majority, found in the shallow waters of the ocean, are encrusting or weakly erect; those occurring in the deeper portions of quiet seas include stemmed, foliate, and ramifying forms, such as finger and cup sponges, the Venus'-flower-basket, and the bath sponge of commerce. Many sponges consist of indistinguishably fused individuals and may weigh hundreds of pounds.

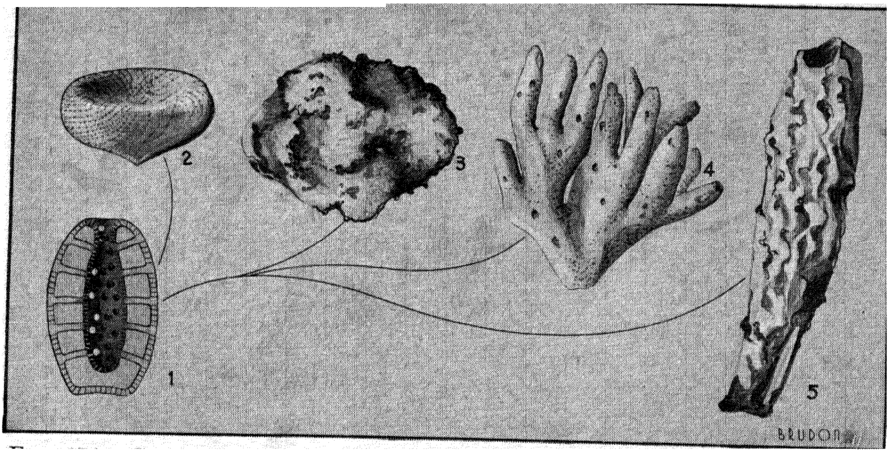

Fig. 174. *Some sponges (Porifera) (1) Generalized sponge, in section, (2) early Paleozoic fossil sponge (Receptaculites); (3) bath sponge (horny skeleton); (4) calcareous sponge (limy skeleton); (5) siliceous sponge (siliceous skeleton).*

About 3,000 species of sponges have been described.

Phylum III. Coelenterata (sël en′ ter ā′ ta), Greek, *koilos*, hollow; *enteron*, intestine.

The hydroids, jellyfishes, sea anemones, and corals. Simple Metazoa, mostly marine. Exhibiting usually the following characters:

Body wall diploblastic, with an outer germ layer, the ectoderm, and an inner, the entoderm, enclosing a third jellylike, noncellular layer, the mesoglea, which may become very thick in some forms (jellyfish). Somatic cell differentiation marked. Radial symmetry, modified by an increasing tendency toward bilateral symmetry in the higher species of the phylum. No metamerism. Possessed of a coelenteron—a single body cavity lined with entoderm and opening to the outside by a mouth but lacking an anus. The typical sac-type of body organization occurs throughout but is modified to form either a tubular polyp, or a bell- or umbrella-shaped medusa (jellyfish).

Among the features peculiar to this group are an alternation of generations, called *metagenesis,* whereby a usually sessile and colonial asexual polyp generation produces, by budding, the sexual, often free-swimming medusa or jellyfish generation; and the presence of tentacles furnished with highly specialized stinging cells known as *nematocysts.*

The coelenterates are divided into three classes. With the exception of the Portuguese man-of-war and a few other showy forms, the first class, Hydrozoa, comprising the freshwater Hydra, the marine colonial hydroids (Obelia, etc.), small jellyfish, and the hydrocorals, is known chiefly to students of aquatic life. The group consists of thousands of species, some very common and many very beautiful.

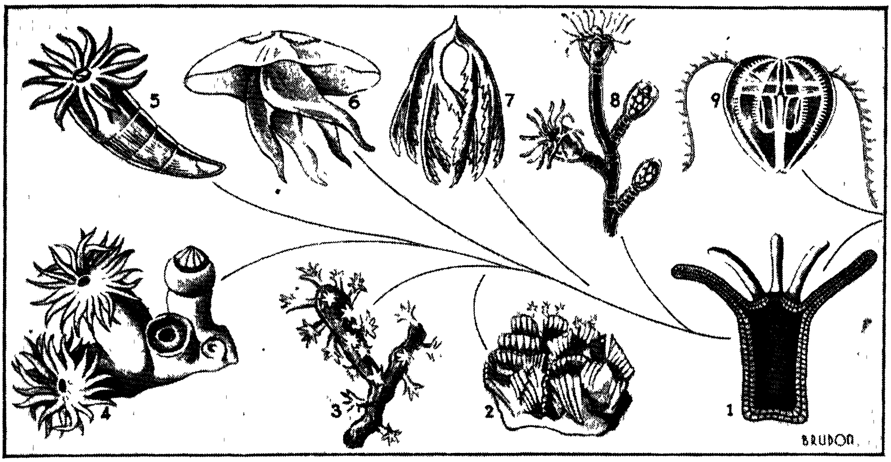

FIG. 175. *Coelenterata and Ctenophora.* (1) *generalized coelenterate of polyp type (Hydra)*; (2) *an early Paleozoic fossil tabulate coral (chain-coral, Halysites)*; (3) *horny coral*; (4) *stony coral*; (5) *early Paleozoic fossil cup coral (Zaphrentis)*; (6) *jelly-fish or medusa*; (7) *early Paleozoic fossil graptolite colony*; (8) *colonial hydroid (Obelia)*; (9) *ctenophore, the sea walnut.*

To the second class, Scyphozoa, belong practically all the large jellyfish, familiar seashore sights, their often vivid coloring and brilliant phosphorescence making them conspicuous.

Sea fans, sea feathers, most of the corals, and all the sea anemones make up the last class, Anthozoa, some members of which are familiar to all visitors to the seashore.

Approximately 4,500 species of this phylum are known.

Phylum IV. Ctenophora (tē nŏf′ or a), Greek, *ktenos,* comb; *phoros,* bearing.

The sea walnuts or comb jellies. Relatively simple marine metazoa, exhibiting the following characters:

Body wall of adults primarily diploblastic. However, the jellylike mesoglea, separating the ectoderm from the entoderm, contains some muscle cells that originate embryologically in such a manner as to suggest that they are mesodermal. Hence the Ctenophora is often placed as the most primitive of the triploblastic phyla. Radial combined with bilateral symmetry (sometimes called *biradial symmetry*). A highly specialized coelenteron consisting of an aboral cavity that connects with a system of tubes and canals, and an oral cavity (reached through the single opening, the mouth), each flattened on a plane at right angles to the other.

Among the features peculiar to the phylum are the tentacles equipped with adhesive cells instead of nematocysts and the possession of eight meridionally arranged rows (combs) of swimming plates.

The Ctenophora is a minor phylum composed of exclusively marine jellyfishlike animals, formerly classified as Coelenterata. Ctenophora differ from coelenterates in their general body form (bell-shaped or ribbonlike), their tendency toward the triploblastic type of organization, the absence of nematocysts, and biradial symmetry. There is no mistaking ctenophores seen in life: they are remarkably transparent and are among the most beautiful of all sea animals. During the day, the plate rows are irridescent with reflected light, and at night, the entire animal may be vividly phosphorescent.

One hundred species are known.

Phylum V. Platyhelminthes (plat′ e hel min′ thēz), Greek, *platys,* broad; *helminthos,* worm.

The flatworms. Intermediate metazoa, exhibiting the following characters.

Body triploblastic, much flattened dorsoventrally. Flatworms possess a definite third layer of cells, the mesoderm, and have developed from this layer various systems of organs. Bilateral symmetry. No true metamerism, unless the tapeworm be considered an "individual" rather than a colony of individuals.

Digestive system essentially a coelenteron, with a single opening, the mouth. In many species, however, the coelenteron has been modified into a highly branched gastrovascular system. No coelom; no anus. Digestive system entirely lacking in the tapeworms because of their parasitic mode of life.

Among the special features of the phylum are the presence of "flame cells" in the excretory system and the fact that individuals are for the most part hermaphroditic, having both male and female reproductive systems.

The Platyhelminthes include both free-living and parasitic species. The former, of which Planaria is an example, are the less numerous and occur principally in fresh or salt water. The parasites include the flukes and tapeworms, most of which live within the bodies of other animals and many of which cause diseases of man and domestic animals. As in the instance of other parasitic animals, they show great specialization related to their peculiar mode of life, such as enormously increased powers of reproduction and extremely complicated life cycles that in certain cases involve three or four different larval forms each requiring a different host.

Approximately 5,000 species of the phylum are known.

Phylum VI. Nemathelminthes (nĕm′ a thel min′ thēz), Greek, *nematos*, thread; and *helminthos*, worm.

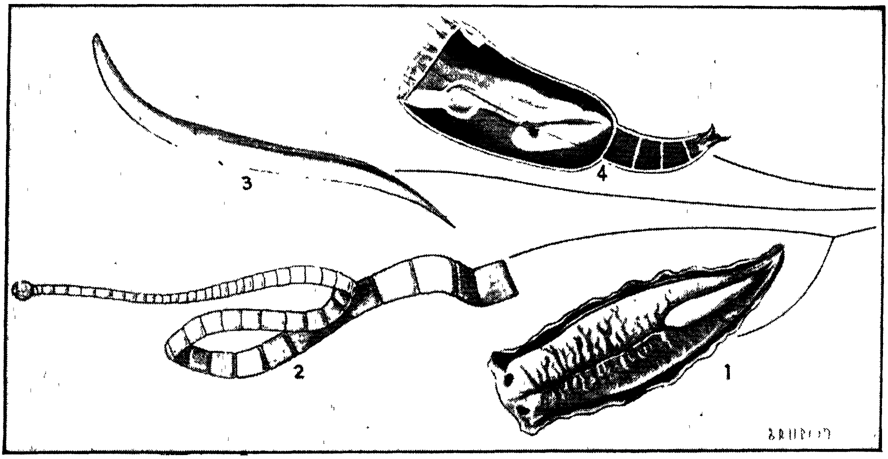

FIG. 176 *Platyhelminthes, Nemathelminthes, and Rotifera.* (1) (2) *Platyhelminthes: Planaria and tapeworm;* (3) *Nemathelminthes, roundworm* (*Ascaris*); (4) *rotifer* (*Hydatina*)

The unsegmented roundworms or threadworms. Intermediate metazoa, exhibiting for the most part the following characters:

Triploblastic; bilateral symmetry; no metamerism. Digestive tract complete, both mouth and anus being present. Body cavity or coelom present, though incomplete or atypical in not being lined throughout with mesoderm. Body elongated, cylindrical, usually pointed at both ends. Body organization of the most primitive tube-within-tube type.

These smooth, glistening, slender worms occur in large numbers, both as regards species and individuals, in soil and in fresh and salt water and as parasites in plants and animals. The common vinegar eel is an example of the free-living roundworms; the horsehair snake is typical of others that spend part of their lives as parasites and another part as free-living organisms: and the hookworms and Ascaris are roundworms completely adapted to parasitic existence.

Approximately 80,000 species of Nemathelminthes have been described, and partly because of the extreme difficulty of recognizing species in this group, it is probable that many more thousands remain to be discovered.

Animals of Uncertain Relationships

A number of groups of animals are considered together here because their relationships to other animals and to each other, as well as their position in an evolutionary sequence, are uncertain. All are triploblastic and bilaterally symmetrical, and all show a degree of organization at least as complex as that of the Platyhelminthes and Nemathelminthes.

Nemertinea (nĕm′ er tin′ e a). Worms, mostly marine, probably related to the flatworms. Important characteristics: a protrusible proboscis that lies in an anterior sheath (the latter considered by some the coelom); digestive tract tubelike, with both mouth and anus; a blood-vascular system. They are the most primitive animals with a circulatory system.

Rotifera (ro tĭf′ er a). Rotifers or wheel animalcules. Minute but complex animals, most of which live in fresh water, although some are marine and a few parasitic. Movements of cilia at the anterior end suggest rotating wheels. Digestive tract tubelike, with both mouth and anus; easily visible chitinous jaws present within pharynx; 1,000 species.

Bryozoa (brī′ o zo′ a). Moss animals. Small, sessile, unsegmented, mostly colonial animals, living in both fresh and salt water, though more abundant in the latter. Mouth enclosed in a crown of tentacles, the lophophore, a characteristic structure; intestine U-shaped, with anus near the mouth. Bryzoan colonies often bear a superficial resemblance to hydroid colonies, and many secrete corallike skeletons. This group is sometimes combined with the following one (Brachiopoda) to constitute the phylum Molluscoidea. About 1,200 known species.

Brachiopoda (brak′ i op′ o da). Lamp shells. Body unsegmented nd covered by a calcareous (limy) two-valved shell, which often has the ppearance of an ancient form of lamp. The shells cover the dorsal and entral surfaces instead of the lateral surfaces, as in the clams and mussels phylum Mollusca). The mouth is situated between two spiral ciliated rms (lophophore), which lie coiled within the shell; the ciliated food anal may end blindly or be provided with an anus near the mouth; the ody may be directly moored to the substratum or be attached by a stalk pedicel) from the posterior region. More abundant in past geological eriods than at present, thousands of fossil species being known; 500 ving species, all marine.

Phylum VII. Echinodermata (e kin′ o der′ ma ta), Greek, *echinos*, hedgehog, referring to the spines; *derma*, skin.

Starfishes, brittle stars, sea urchins, sea cucumbers, sea lilies. Complex Metazoa, typically with the following characters:

Triploblastic. No marked metamerism. Adults radially symmetrical (usually on a plan of five antimeres). Inasmuch as larval echinoderms are bilaterally symmetrical, the phylum has probably been derived from bilaterally symmetrical ancestors. A large coelom and distinct alimentary canal that usually, but not always, terminates in an anus.

The following special features of the phylum are notable: skin usually spiny; body wall with calcareous plates (much reduced in the sea cucumbers) that form a protective exoskeleton; a peculiar water-vascular system that, in most forms, constitutes a hydrostatic pressure system that regulates movements of the tube feet (locomotor organs characteristic of this phylum). Circulatory and nervous systems poorly developed.

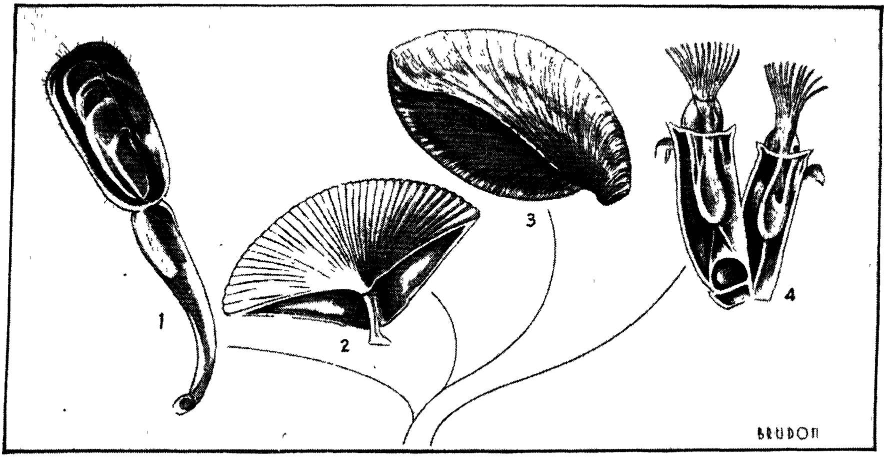

FIG. 177. *Brachiopoda and Bryozoa* (1)–(3) *Brachiopods:* (1) *Lingula, Cambrian to Recent;* (2) *Spirifer, Paleozoic;* (3) *Terebratula, Cenozoic and Recent;* (4) *Bryozoa, two individuals of the colonial Bugula.*

The echinoderms are all marine and constitute a considerable portion of the animal life of the seashore. Among the objects most likely to attract the attention of the shore visitor, particularly if the coast is somewhat rocky, are the five-armed *starfishes* (class Asteroidea). These are often found in abundance, when the tide is low, clinging to rocks and seaweeds. Among the seaweeds that grow below the tidal zone, there may be found somewhat similar animals called *serpent stars* (class Ophiuroidea), which have five slender, wriggling, snakelike arms. Just below the reach of low tide, there occur other related animals, of rounded form, covered with long, coarse spines; these are commonly known as *sea urchins* (Class Echinoidea). The flattened sand dollars are also members of this class. And if one digs in the sand exposed between tides, he may encounter pink or whitish wormlike animals, without distinct appendages but nevertheless able to cling to the hand; some of these belong to a group of the echinoderms known as *sea cucumbers* (class Holothuroidea). The *sea lilies* or feather stars (class Crinoidea) live mostly in deep water.

These five classes of animals, different as they may seem at first glance, are included in this one phylum because they possess in common the features indicated above. Certain indications from the developmental stages of echinoderms suggest that these animals and the chordates had a common ancestry.

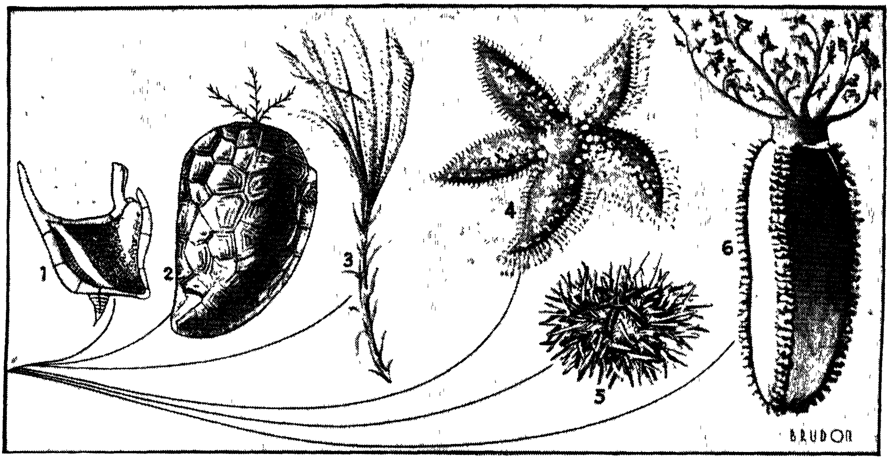

FIG. 178. *Echinodermata.* (1) *Early Paleozoic bilaterally symmetrical fossil cystoid showing chordate-like characters;* (2) *Silurian fossil cystoid;* (3) *sea-lily* (*crinoid*); (4) *starfish* (*asteroid*); (5) *sea urchin* (*echinoid*); (6) *sea cucumber* (*holothuroid*).

Approximately 6,000 modern species of echinoderms are known.

Phylum VIII. Mollusca (mol lus′ ka), Latin, *molluscus*, soft.

Snails, clams, squids, and octopuses. Complex Metazoa, typically exhibiting the following characters:

Triploblastic. Bilateral symmetry, tending toward asymmetry (snails).

Soft-bodied, unsegmented animals without jointed appendages.

Coelom present. Complex respiratory (gills), circulatory, reproductive (monoecious or dioecious) and nervous systems. Digestive system complete with anus. Nervous system variable, not of the ladder or dorsal cord types, exhibiting strong cephalization in certain groups that have very complex organs of sight.

Usually a shell of lime carbonate is present, secreted from the outer surface of an enveloping layer of tissue called the *mantle;* a space, the mantle cavity, separates the main body from the mantle. The shell may be: (1) of *one piece,* pyramidal or coiled (in snails); (2) composed of *two lateral valves* (in clams, etc., called *bivalves*); (3) composed of a series of small *plates* (in Amphineura); (4) *reduced or wanting* (in the squid, octopus, some snails). Even when the shell is rudimentary or absent, the mantle and its cavity are still present. All Mollusca possess a fleshy organ called the *foot,* which, in the snail, is usually a flat sole used for creeping over surfaces; in the clam, is generally a wedge-shaped organ used for plowing in mud or sand; and in the squid, is divided into arms provided with sucking disks and used for seizing prey.

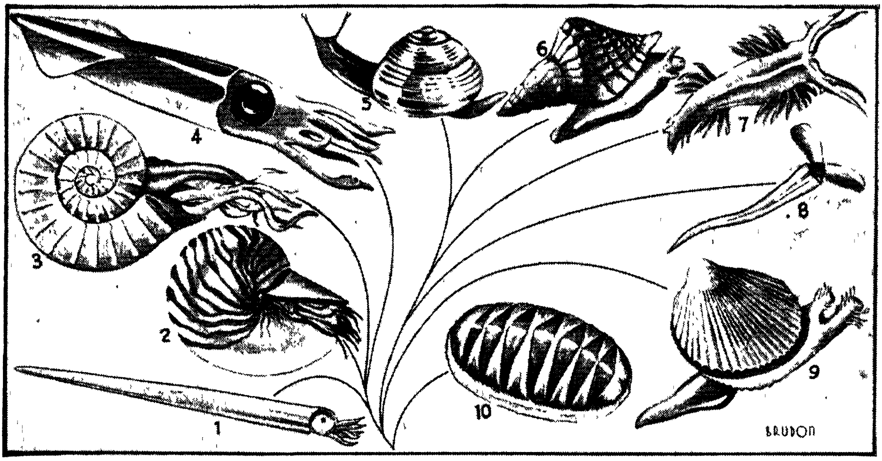

FIG. 179. *Mollusca.* (1)–(4) *Cephalopods:* (1) *primitive fossil type, early Paleozoic* (*Orthoceras*); (2) *pearly nautilus;* (3) *fossil ammonite, Mesozoic;* (4) *squid;* (5)–(8) *Gastropods:* (5) *garden snail;* (6) *marine snail* (*Triton*); (7) *marine snail* (*nudibranch*); (8) *pteropod or wing shell;* (9) *clam* (*pelecypod*); (10) *chiton* (*amphineuran*).

Mollusks are among the more abundant of animals. Many snails and slugs crawl about on land, breathing by means of a sort of lung. Fresh-water ponds and streams are the haunts of numerous species of snails, both lung breathers and gill breathers, as well as of the fresh-water mussels and clams. The sea, however, is the home of the greatest variety of mollusks. The principal classes of this phylum are easily distinguished; they are as follows:

Class 1. The Chitons (Amphineura, am′ fi nu′ ra). These are flattened or wormlike mollusks with obvious bilateral symmetry. The commonest type has the back covered with a shell composed of a longitudinal row of eight curved plates, the joints between which allow the animal to roll up like an armadillo. Chitons are all marine, living mostly on rocky coasts. There are several hundred existing and about 100 known fossil species.

Class 2. The Snails and Slugs (Gastropoda, gas trop′ o da). In this class, there is a well-defined head, and the bilateral symmetry is usually obscured by a one-piece spiral shell; the foot has a flat, crawling sole. Most snails are marine, and many of the most attractive sea shells of our beaches are made by members of this group, some of which live among rocks and others in sand or mud. Some of the marine snails have become pelagic and swim at the surface by flapping their two-winged foot. Most are herbivorous, but many live on decomposing animal matter, and some are predacious. A relatively small number of kinds inhabits fresh water, and the land snails (Pulmonata) have a sort of lung developed from the mantle cavity.

Class 3. The Tooth Shells (Scaphopoda, ska fop′ o da). A small group of marine mollusks with a conical shell, straight or curved, and open at both ends; marine, burrowing in sand and mud.

Class 4. The Bivalve Mollusks (Pelecypoda, pel′ e sip′ o da, or Lamellibranchiata, la mel′ i brank′ i at′ a). A very large group of mollusks, which lack a head, have bilateral symmetry, a shell composed of two lateral valves, and a mantle of two lobes. Largely marine, but some occur in fresh water.

Class 5. The Cephalopods (Cephalopoda, sef′ a lop′ o da). Squids, octopods, nautilus, ammonites, etc. These mollusks have a well-developed head with prominent eyes, the latter closely analogous to but not homologous with the eyes of vertebrates; mouth with horny jaws and a rasping tongue like that of the snails; foot transformed into a ring of arms or tentacles surrounding the mouth, prehensile and often furnished with sucking disks and hooks; the mantle muscular, its cavity so arranged that the water contained in it can be squirted out through a "funnel" or "siphon," thus propelling the animal backward. The earlier forms all covered with a straight-conical or coiled, chambered shell; shell reduced or absent in most modern forms.

The fossil record of this group is unusually complete; it is given in brief synopsis in discussing the ammonites of the Mesozoic era. Surviving cephalopods are the squids, cuttlefishes, nautilus and octopus. These are some of the most peculiar and fascinating of animals. Some of the deep-sea squids are the largest of all invertebrates.

Many of the mollusks are of economic importance. Some are eaten (oysters, clams, scallops); the shells of others are used for making buttons and for other commercial purposes; and the pearl oysters are the basis for an important industry. About 80,000 modern species of mollusks have been described, and fossil forms are extremely numerous. The snails appear to be the largest group in existence today and are now at the climax of their development.

Phylum IX. Annelida (an nĕl′ i da), Latin, *annelus*, ring.

Segmented worms such as earthworms, marine worms, and leeches. Highly developed intermediate metazoa, typically exhibiting the following characters.

Triploblastic; bilateral symmetry; metamerism well developed, each metamere (somite or segment) more or less similar to the others. Blood vessels, excretory organs (nephridia), and nervous system segmentally arranged. Tube-within-tube type of organization; alimentary canal differentiated into organs; distinct coelom present, lined with mesoderm and often divided into chambers by transverse metameric partitions.

A complex circulatory system present, operating with respiratory organs (external gills) in some of the marine Annelida; ventral double nerve cord with nerve centers (ganglia) in each metamere, constituting a "ladder type" of central nervous system, in front encircling the alimentary canal to form a "brain" above it. When present, the appendages not jointed or segmented but in the form of spines (earthworms), fleshly flaps (marine Annelida), or suckers (leeches).

Most annelids are marine, but many live in fresh water or in the soil or other moist places. A few are parasitic, notably the leeches, many of which are external parasites on the bodies of aquatic animals and a few on terrestrial animals.

The common earthworm is the most frequently studied annelid. Earthworms are soft-bodied and "slimy." They live in moist earth and venture out of their burrows chiefly on damp nights. The burrows usually extend about 2 feet beneath the surface. The worms can force their way through soft ground but must eat their way through harder soil. The earth eaten passes through the alimentary canal and is deposited on the surface of the ground as "castings." Decaying vegetable matter in the soil provides food; the worms also eat leaves and other surface vegetation, which they drag into their burrows at night. Thus earthworms continually honeycomb the soil, making it more porous, permitting better penetration of air and moisture, and increasing its fertility.

About 8,000 species of Annelida have been described. The Annelida are closely related to and perhaps are the ancestors of the Arthropoda.

Phylum X. Arthropoda (ar throp′ o da), Greek, *arthron*, joint; *podos*, foot.

Crustaceans, centipedes, insects, spiders, and their allies. Complex Metazoa, typically exhibiting the following characters:

Triploblastic; bilateral symmetry; metameric. Although the body cavity is continuous and without transverse septa, metamerism is shown internally in the arrangement of the nervous system, muscles, heart, and other organs. Groups of segments tend to fuse or specialize into larger regions, such as head, thorax, and abdomen, or into combinations of these (cephalothorax). With the exception of the vertebrates, arthropods are the most highly developed metameric animals. Coelom present but much reduced, its place being taken by an extensive blood space, the hemocoele.

Jointed appendages. Usually a hard exoskeleton. Ladder type of nervous system (as in Annelida), with a tendency toward cephalization (concentration of ganglia at anterior end). Usually with well-developed and segmented head appendages (antennae, mouth parts, etc.). A main longitudinal blood vessel ("heart") dorsal to the alimentary canal. Respiration by gills or tracheae.

The arthropods comprise about four-fifths of all the known species of animals. Many occur in marine and fresh-water habitats, but they are best represented on land. They may be regarded as the dominant animals of today, if numbers of different species and numbers of individuals are accepted as criteria of dominance. Approximately 650,000 species are known, of which 600,000 are insects. This huge assemblage of animals may be divided into classes, as follows:

Class 1. The Crustacea (crus tā′ she a). Mostly aquatic; usually with gills; chitinous exoskeleton stiffened with limy deposits; two pairs of antennae; appendages typically two-branched (biramous); first two body regions (head and thorax) commonly fused into one (cephalothorax). Examples: lobsters, crabs, crawfishes, shrimps, barnacles, water fleas, sow bugs.

Class 2. The Arachnida (a rak′ ni da). Metameres reduced by fusion; no antennae; four pairs of legs; respiration generally by tracheae or book lungs or both (by book gills in the few existing aquatic forms). Examples: spiders, scorpions, ticks, mites, horseshoe crabs, eurypterids.

Class 3. The Onychophora (on′ i kof′ o ra). Soft-bodied, wormlike, primitive forms, discontinuously distributed in the tropics. Apparently intermediate between the metameric worms (Annelida) and the arthropods; excretory system of the annelid type (a series of paired nephridia); respiratory organs resembling the tracheae of the insects and myriapods; external appendages exhibiting weak segmentation. Few species. Example: Peripatus.

Class 4. The Myriapoda[1] (mĕr′ i ap′ o da). Body long, and, except for the head, composed of more or less similar segments, each of which bears one pair[2] of jointed appendages. Head with one pair of antennae and two or three pairs of mouth parts. Terrestrial, breathing by means of tracheae. Examples: centipedes, millipedes.

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[1] While it is convenient in a nontechnical account to include the centipedes, millipedes, and certain other groups of superficially similar organisms in the single class Myriapoda, modern classifications recognize the important differences that exist between these groups by breaking the old Myriapoda into at least four smaller classes.

[2] In the millipedes there appear to be two pairs of appendages to each segment, but this results from the fact that each apparent body segment is composed of two fused somites.

Class 5. The Insecta (in sek′ ta). Metameres grouped into three main body divisions (head, thorax, and abdomen); one pair of antennae; complicated biting or sucking mouth parts; three pairs of legs; wings usually present. Respiration by means of tracheae or tracheal gills. Mainly terrestrial, with certain groups secondarily adapted to fresh water. A high degree of social development has been reached in a few groups. The class is of great economic importance. Examples: grasshoppers, termites, fleas, moths, bees. Some important orders are given below:

Name of Order	*Included Types*
Aptera	Primitive wingless insects
*Palaeodictyoptera	Ancestral winged insects
Odonata	Dragonflies
Orthoptera	Cockroaches, walking sticks, praying mantids, grasshoppers, katydids, crickets
Isoptera	Termites
Hemiptera	True bugs
Homoptera	Cicadas or harvest locusts, scale insects, white flies, leaf hoppers
Lepidoptera	Butterflies and moths
Coleoptera	Beetles
Diptera	Flies, mosquitoes
Hymenoptera	Ants, wasps, bees

Phylum XI. Chordata (cor dā′ ta), Greek, *chorde*, cord *i.e.*, the notochord.

The backboned animals and their allies. The vertebrates constitute the majority of the chordates and include man and all his nearest relatives. The chordates are the most highly developed of all animals. Among their general characteristics are the following:

Triploblastic. Bilateral symmetry. Metamerism evident. Coelom present; organ systems highly developed. Endoskeleton always present at some stage. Its characteristic form is the notochord, a longitudinal dorsal rod, replaced to varying degrees in higher forms by the centra of a series of vertebrae, which together constitute a vertebral column (backbone). Respiration always involving the pharynx; gill clefts present in this region at some stage of development (these persistent only in the classes below Amphibia). Central nervous system composed of a dorsal hollow nerve cord, the anterior portion of which forms the brain in the vertebrates.

There are about 70,000 existing species of Chordata, of which all but a relatively small number are vertebrates. Four subphyla are commonly recognized, but the first three of these may be combined under the name

Protochordata. The remaining subphylum, the Vertebrata, may be conveniently divided into eight classes, though more than eight are often made.

Subphylum *A*. The Primitive Chordates (Protochordata, pro′ to-kor dā′ ta). This subphylum includes the lower chordates, for the most part unrecognizable as such except on the basis of their embryology. They possess, in some stage, what are believed to be the homologues of notochord, gill slits, and hollow dorsal nerve cord; but they lack a brain case, vertebral column, paired appendages, true ventral heart, and hemoglobin in the blood. There are three classes:

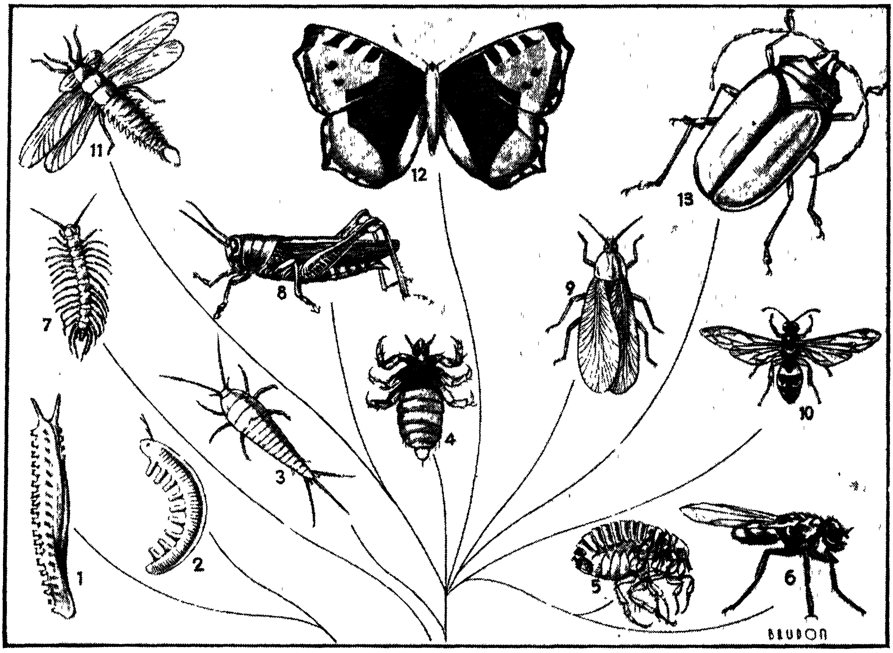

FIG. 180. *Onychophora, Myriapoda, and Insecta.* (1) (2) *Onychophora:* (1) *modern Peripatus;* (2) *marine Peripatus-like fossil from the Cambrian;* (3)–(6) (8)–(13) *Insects:* (3) *silver fish* (*primitive wingless insect*); (4) *body louse;* (5) *flea;* (6) *fly;* (8) *grasshopper;* (9) *primitive fossil insect from the Carboniferous, related to the cockroaches;* (10) *wasp;* (11) *primitive fossil insect* (*paleodictyopteran*) *from the Carboniferous;* (12) *butterfly;* (13) *beetle;* (7) *Myriapod* (*a centipede*).

Class 1. The Acorn Worms (Hemichordata, hem′ i kor dā′ ta). Wormlike marine animals with a muscular proboscis and collarlike neck region; notochord short, not typical, forming a blind tube extending forward into the proboscis from the dorsal wall of the alimentary canal; paired lateral gill slits present. Some students of the chordates would exclude this group from the phylum. *Example:* Balanoglossus.

Class 2. The Sea Squirts or Tunicates (Urochordata, you′ ro kor-dā′ ta). Solitary or colonial marine animals with a saclike covering called the *tunic.* Notochord absent in adult, present in the tail of the tadpolelike larva. Adult either fixed (sessile) or in a few forms free-swimming and pelagic.

Class 3. The Lancelets (Cephalochordata, sef′ al o kor dā′ ta). Amphioxus, a small fishlike marine animal, with elongated body in which metamerism is evidenced by the V-shaped muscle segments of the trunk. Notochord well developed, extending practically the full length of the body. Gill slits numerous. Without true head or brain. A good swimmer but spending most of time buried in sand with anterior and posterior ends protruding; beating cilia cause a stream of water to flow into the mouth and out the gill slits, food particles being retained by entanglement with a gelatinous secretion of the pharynx.

Subphylum *B.* The Vertebrates (Vertebrata, ver′ te brā′ ta). Notochord, if persistent, surrounded by cartilage; if not persistent, replaced by a vertebral column made of cartilage or bone. A brain case (cranium) present and, typically, two pairs of appendages (forelimbs and hindlimbs), each arising from several somites and supported by an internal skeleton. Front end of neural tube enlarged into a brain, the remainder forming the spinal cord. Includes the following classes, the first six of which are cold-blooded, the last two warm-blooded:

*Class 1. The Ostracoderms (Ostracodermata, os′ trak o derm′ a ta). The most primitive vertebrates, known only as fossils from the early Paleozoic. Without jaws, body with external head armor and lateral plates in addition to internal skeleton; eyes dorsal. There are actually several different types of ostracoderms, constituting four or five orders.

Class 2. The Lampreys and Hagfishes (Cyclostomata, sī′ klo sto′-ma ta). Eel-like forms with rounded mouths, no jaws, numerous gill slits, no paired appendages. Notochord persistent but covered with a cartilaginous sheath. Largely marine, a few types in fresh water. The hagfishes bore into dead or disabled fish by means of a special drilling apparatus and clean out the body, leaving only a shell; the lampreys attach themselves to the outsides of other aquatic vertebrates by the sucking mouth and rasp off the flesh.

Class 3. The Sharks and Rays (Elasmobranchii, e lăz′ mo brank′ ē ī). All marine. Skeleton cartilaginous; notochord persistent, partially replaced by centra of vertebrae. Jaws present (as in all succeeding classes). Numerous gill slits, exposed or covered only by a flap of skin. Fins paired. Skin with imbedded denticles or "placoid scales," having the structure of a tooth. Heart two-chambered. Includes the sharks, the skates, sawfishes, sting rays or stingarees, electric rays, eagle rays or sea vampires, and chimeras. The extinct Arthrodira were probably related to the ancestors of the sharks.

Class 4. The True or Bony Fishes (Pisces, pis′ ēz). Cold-blooded aquatic vertebrates with internal skeleton bony or partially bony; gills covered by a bony flap (operculum); scales usually present, of ganoid type in primitive forms, in modern fishes (teleosts) thin and horny (cycloid or ctenoid), never of "placoid" type. Paired fins usually present. Heart two-chambered, approaching the three-chambered condition in Dipnoi.

Subclass 1. Choanichthyes. Fishes with internal nostrils enabling them to breathe air without opening the mouth. This subclass includes the Dipnoi, or lungfishes, with fan-shaped tooth plates, lacking the maxillary and premaxillary bones of the upper jaw and having elongated leaflike paired fins with a central skeletal axis; and the *Crossopterygii, or lobe-finned fishes, with marginal teeth on the maxillary and premaxillary bones and fins with a fleshy base that contains the skeletal elements of the pentadactyl limb; all extinct, but ancestral to Amphibia.

Subclass 2. The Ray-finned Fishes (Actinopterygii), without internal nostrils; fins with a very short base and consisting chiefly of a membranous web supported by slender horny rays. The principal group of the ray fins is the order Teleosti, the modern fishes, comprising more than 90 per cent of all living species of fishes; in this group, the scales are thin and horny or often are lost altogether, and the swim bladder is no longer used for breathing but is a purely hydrostatic organ.

The first four classes of the Vertebrata are sometimes all grouped together into the single category of *Fishes*.

Class 5. The Amphibians (Amphibia, am fib′ e a). Salamanders, frogs and toads, blindworms, and the extinct *stegocephalians. Cold-blooded vertebrates partially adapted to land life, with two pairs of pentadactyl limbs except when these have been lost through degeneration; skull with double occipital condyle; skin smooth or rough and rich in glands that keep it moist; modern amphibians without skin plates or scales except for traces imbedded in the skin of the blindworms, extinct types with bony plates buried in the skin (dermal, not epidermal structures); respiration usually by gills in the young, by lungs and skin in the adult; heart three-chambered in the adult; eggs, with few exceptions, laid in water and larval stages aquatic, most adults partly or completely terrestrial but some aquatic throughout life.

The Paleozoic amphibians, which we have referred to as the *Stegocephalia, are also called **labyrinthodonts,* because of their large teeth with the enamel layer complexly infolded. These were the ancestors of the reptiles. They were not, however, the only amphibians present in the late Paleozoic. A second group of small salamanderlike forms had features in their skulls and vertebrae strongly suggesting that they were the ancestors of the modern orders Caudata (salamanders) and Salientia (frogs and toads). Still a third Paleozoic order is thought to have given rise to the modern Apoda (blindworms or caecilians), which are small, burrowing, wormlike, legless tropical forms. They are more completely terrestrial than most other modern amphibians, and some of them are ovoviparous, the male possessing a copulatory organ.

Class 6. The Reptiles; Reptilia (rep til′ e a). Lizards, snakes, turtles, alligators, and crocodiles, Sphenodon, and numerous *extinct groups of the Paleozoic and Mesozoic. Cold-blooded, fully terrestrial vertebrates (except for secondary adaptations to aquatic existence), without gills at any time; independent of the water for breeding, through possessing a shelled egg along with internal fertilization; oviparous or ovoviparous; skin with few glands, covered by horny epidermal scales unlike the dermal scales of fishes, making it dry and waterproof; with two pairs of pentadactyl limbs except when these have been lost through degeneration, the toes usually armed with claws—the forerunners of the claws, hoofs, and nails of birds and mammals; lung breathing aided by ribs; heart three-chambered, the ventricle partly subdivided, thus tending toward the four-chambered condition and complete double circulation; third eyelid, pineal eye, and depressed eardrum developed; skull with a single median occipital condyle.

The classification of the reptiles has been dealt with in detail in describing the life of Mesozoic times. Here it will suffice to list the principal subdivisions of the class.

Subclass 1. Anapsida (an ap′ si da). Without temporal openings in the skull.
  *Order 1. The Paleozoic stem reptiles (Cotylosauria, co til′ o-saur′ e a).
  Order 2. The turtles (Chelonia, che lōn′ ē a).
*Subclass 2. Synapsida (sĭn ap′ si da). With a pair of lateral temporal openings in the skull.
  *Order 1. The ship lizards (Pelycosauria, pel′ i co saur′ e a).
  *Order 2. The mammallike reptiles (Therapsida, ther ap′ si da).
*Subclass 3. The Ichthyosaurs (Parapsida, par ap′ si da).
*Subclass 4. The Plesiosaurs (Synaptosauria, sĭn′ ap to saur′ e a).
*Subclass 5. Diapsida (dī ap′ si da). With both dorsal and lateral temporal openings in the skull.
 A. Lizardlike Reptiles.
  Order 1. The tuatara, Sphenodon (Rhynchocephalia, rin′ ko se-fāl′ e a).
  Order 2. The lizards and their allies (Squamata, squa mā′ ta).

*Suborder 2. The mosasaurs (Mosasauria, mo′ sa saur′ e a).
Suborder 3. The snakes (Ophidia, o fid′ e a).
B. The Archosaurs.
*Order 1. The ancestral archosaurs (Thecodontia, the′ ko dont′-e a).
*Order 2. The phytosaurs (Phytosauria, fī′ to saur′ e a).
Order 3. The crocodiles and alligators (Crocodilia, krock′ o dil′ e a).
*Order 4. The flying reptiles or pterodactyls (Pterosauria, ter′ o-saur′ e a).
*Order 5. The saurischian dinosaurs (Saurischia, saur isk′ e a).
*Order 6. The ornithischian dinosaurs (Ornithischia, orn′ ith-isk′ e a).

Class 7. The Birds (Aves, ā′ vēz). Warm-blooded, air-breathing vertebrates, with primary adaptations for flight; body covered with feathers; forelimb three-fingered, modified into a wing (in a few groups this secondarily specialized for swimming, or vestigial); heart four-chambered, with complete double circulation, single right aortic arch preserved; respiration by means of highly perfected lungs, their capacity increased by accessory air sacs that penetrate the coelomic cavity and the interior of the bones, reducing relative weight and thus aiding in flight; all modern birds with a syrinx or voice-organ situated at the junction of the trachea with the two bronchi, taking the place of the larynx as a sound-producing structure; skeleton made rigid by fusion of many of its bones, the breastbone in all strong fliers enlarged for insertion of massive flight muscles; body streamlined; a single left ovary and oviduct retained in most forms; eggs and egg membranes essentially reptilian, but the eggs usually incubated by the heat of the parent's body, and parental care highly developed in the majority of modern forms.

The birds form a large and highly successful group, which is apparently not even yet at its zenith. Relationships among modern birds are so close and the assemblage is so homogeneous that it is not easy to subdivide the existing species into numerous well-defined groups. The differences that distinguish the orders and families are much less pronounced than in the other classes of vertebrates. For our purposes, the following outline classification must suffice:

*I. The Reptilian Birds. Archaeopteryx and Archaeornis, Jurassic.
II. The True Birds (Neornithes, ne orn′ i thēz).
*Section 1. The toothed flying birds (Ichthyorniformes, ik′ thi-orn′ i form′ ēz). Ichthyornis, Cretaceous.
*Section 2. The toothed diving birds (Hesperornithes, hes′ per-orn′ ith ēz). Hesperornis, Cretaceous.
Section 3. The running birds (Ratitae, ra tī′ tē), with six orders of modern birds, all flightless: Ostriches, rheas, emus and cassowaries,

kiwis, and the recently extinct moa of New Zealand and elephant bird (Aepyornis) of Madagascar.

Section 4. The keeled or flying birds (Carinatae, kar′ in āt′ ē), with 16 orders of modern birds comprising nearly 12,000 species, most of them with a strongly carinate breastbone and well-developed powers of flight.

Class 8. The Mammals, or Hairy Vertebrates (Mammalia, mam-āl′ e a). Warm blooded, air-breathing vertebrates with bodies more or less covered with hair. The skin contains sweat, oil, and mammary glands, the secretion of the latter (milk) serving to nourish the young. The skull has two occipital condyles; the lower jaw consists of a single bone, the dentary, which articulates with the squamosal bones; the articulate and quadrate bones of the ancestral jaw hinge are transformed into the malleus and incus bones of the middle ear, the third bone (stapes) being an inheritance from the reptiles. The teeth are imbedded in sockets in the jawbone and are of two sets (milk teeth and permanent teeth); they are differentiated into incisors, canines, premolars, and molars. The ear is usually furnished with an external trumpet, the tympanic membrane lies at the bottom of a tube, and the cochlea of the inner ear (the auditory sense organ) is spirally coiled except in the monotremes. There are fleshy cheeks and lips covering the edges of the jaws and teeth.

The neck nearly always has only seven vertebrae; the centra of the vertebrae are separated by cartilaginous disks; the ribs articulate with the vertebrae by two heads; the first digit of forelimbs and hind limbs has two bones, all the remaining digits three (a lower number than in the reptiles). The thoracic and abdominal cavities are separated by a muscular diaphragm that aids in breathing. The brain is relatively large, the cerebrum and especially the cerebral cortex (neopallium) greatly enlarged, and the two cerebral hemispheres are connected by the corpus callosum, a massive bundle of fiber tracts (rudimentary in marsupials and absent in monotremes). The cerebellum is large, complex, and solid.

A cloaca (combined anal and urinogenital opening) is absent except in monotremes; a urinary bladder is present. A penis is always present. The eggs are alecithal, microscopic (except in monotremes); they develop in a uterus (except in monotremes), to the walls of which the embryo is attached by a placenta (except in the monotremes and most marsupials); the young are "born alive" (except in monotremes).

The classification of the mammals has been given in some detail in the synoptic table of the animal kingdom and will not be repeated here.

APPENDIX B

A List of Books for Browsing, Collateral Reading, and General Reference

I. GENERAL BIOLOGY

Goldschmidt, Richard: *Ascaris: The Biologist's Story of Life,* Prentice-Hall, Inc., New York, 1937.

Parshley, H. M : *Biology,* John Wiley & Sons, Inc., New York, 1940.

Plunkett, C. R.: *Outlines of Modern Biology,* Henry Holt and Company, Inc., New York, 1930.

Shull, A. F., G. R. LaRue, and A. G. Ruthven: *Principles of Animal Biology,* 5th ed., McGraw-Hill Book Company, Inc., New York, 1941.

Wells, H. G., J. S. Huxley, and G. P. Wells: *The Science of Life,* Doubleday, Doran & Company, Inc., New York, 4-vol. ed., 1931; 1-vol. ed., 1935.

Williams, S. H.: *The Living World,* The Macmillan Company, New York, 1937.

II. THE STRUCTURE AND FUNCTIONING OF THE HUMAN BODY

Amberson, W R., and D. C. Smith: *Outline of Physiology,* F. S. Crofts & Co., New York, 1939.

Borsook, Henry: *Vitamins,* The Viking Press, New York, 1941.

Cannon, W. B.: *The Wisdom of the Body,* W. W. Norton & Company, Inc., New York, 1932.

Carlson, A. J., and V. Johnson: *The Machinery of the Body,* University of Chicago Press, Chicago, 1937.

Clendenning, Logan: *The Human Body,* 3d ed., Alfred A. Knopf, Inc., New York, 1937.

Gerard, R. W.: *The Body Functions,* John Wiley & Sons, Inc., New York, 1941.

Jennings, H. S.: *The Biological Basis of Human Nature,* W. W. Norton & Company, Inc., New York, 1930.

Romer, A. S.: *Man and the Vertebrates,* University of Chicago Press, Chicago, 1933.

Walter, H. E.: *Biology of the Vertebrates: A Comparative Study of Man and His Animal Allies,* The Macmillan Company, New York, 1928, and subsequent printings.

Williams, J. F.: *Atlas of Human Anatomy,* Barnes & Noble, Inc., New York, 1935.

III. THE STRUCTURE AND FUNCTIONING OF PLANTS

Brown, W. H.: *The Plant Kingdom,* Ginn and Company, Boston, 1935.

Robbins, W. W.: *The Botany of Crop Plants,* 3d ed., The Blakiston Company, Philadelphia, 1931.

Russell, E. J.: *Soil Conditions and Plant Growth,* 6th ed., Longmans, Green and Company, New York, 1932.

Skene, MacGregor: *The Biology of Flowering Plants,* The Macmillan Company, New York, 1932.

Thatcher, R. W.: *The Chemistry of Plant Life,* McGraw-Hill Book Company, Inc., New York, 1921.

Wilson, C. L., and J. M. Haber: *Plant Life,* Henry Holt and Company, Inc., New York, 1935.

IV. REPRODUCTION

Pycraft, W. P.: *The Courtship of Animals,* 2d ed., Hutchinson & Co., Ltd., London, 1933.

Romer, A. S.: *Man and the Vertebrates,* University of Chicago Press, Chicago, 1933.

Shull, A. F., G. R LaRue, and A. G. Ruthven: *Principles of Animal Biology,* 5th ed., McGraw-Hill Book Company, Inc., New York, 1941

Skene, MacGregor: *The Biology of Flowering Plants,* The Macmillan Company, New York, 1932.

Walter, H. E.: *Biology of the Vertebrates,* The Macmillan Company, New York, 1928, and subsequent printings.

Wilson, C. L., and J. M. Haber: *Plant Life,* Henry Holt and Company, Inc., New York, 1935.

V. GENETICS

Babcock, E. B., and R. E. Clausen: *Genetics in Relation to Agriculture,* McGraw-Hill Book Company, Inc., New York, 1918.

Dunn, L. C.: *Heredity and Variation,* The University Society, Inc., New York, 1934.

East, E. M : *Biology in Human Affairs,* McGraw-Hill Book Company, Inc., New York, 1931.

Holmes, S. J.: *Human Genetics and Its Social Import,* McGraw-Hill Book Company, Inc., New York, 1936.

Jennings, H. S.: *The Biological Basis of Human Nature,* W W. Norton & Company, Inc., New York, 1930

Shull, A. F.: *Heredity,* 3d ed., McGraw-Hill Book Company, Inc , New York, 1938.

Snyder, L. H.: *The Principles of Heredity,* 2d ed , D C Heath and Company, Boston, 1940.

V. EVOLUTION IN GENERAL

Beddard, F. E.: *Earthworms and their Allies,* Cambridge University Press, London, 1912.

Berry, E. W.: *Tree Ancestors: A Glimpse into the Past,* The Williams & Wilkins Company, Baltimore, 1923.

Crampton, H. E.: *The Coming and Evolution of Life,* The University Society, Inc , New York, 1931.

Darwin, Charles: *The Origin of Species by Means of Natural Selection,* John Murray, London, 1859, and many subsequent editions.

Gadow, Hans: *The Wanderings of Animals,* Cambridge University Press, London, 1913.

Knowlton, F. H.: *Plants of the Past,* Princeton University Press, Princeton, N. J., 1927.

Lull, R. S.: *Fossils,* The University Society, Inc., New York, 1931.

———: *Organic Evolution,* rev. ed., The Macmillan Company, New York, 1932.

Mason, Frances (editor): *Creation by Evolution,* The Macmillan Company, New York, 1928.

Raymond, P. E.: *Prehistoric Life*, Harvard University Press, Cambridge, Mass., 1939.

Romer, A. S.: *Man and the Vertebrates*, University of Chicago Press, Chicago, 1933.

Schuchert, C., and C. O. Dunbar: *Outlines of Historical Geology*, John Wiley & Sons, Inc., New York, 1941.

Shull, A. F.: *Evolution*, McGraw-Hill Book Company, Inc., New York, 1936.

VI. THE EVOLUTION OF MAN

Bishop, C. W., C. G. Abbott, and Aleš Hrdlička: "Man from the Farthest Past," *Smithsonian Scientific Series*, Vol. 7, 1930.

Clark, W. E. LeGros: *Early Forerunners of Man*, William Wood & Company, Baltimore, 1934.

Coon, C. S.: *The Races of Europe*, The Macmillan Company, New York, 1939.

Dixon, R. B.: *The Racial History of Man*, Charles Scribner's Sons, New York, 1923.

Haddon, A. C.: *The Wanderings of Peoples*, Cambridge University Press, London, 1912.

———: *The Races of Man and Their Distribution*, The Macmillan Company, New York, 1925.

Hooton, E. A.: *Up from the Ape*, The Macmillan Company, New York, 1931.

———: *Why Men Behave Like Apes and Vice Versa, or Body and Behavior*, Princeton University Press, Princeton, N. J., 1940

MacCurdy, G. G.: *The Coming of Man*, The University Society, Inc., New York, 1935.

Murdoch, G. P.: *Our Primitive Contemporaries*, The Macmillan Company, New York, 1936

Palmer, R. A.: "The North American Indians," *Smithsonian Scientific Series*, Vol. 4, 1929.

VII. THE INTERRELATIONS OF ORGANISMS: ECOLOGY

Bayne-Jones, Stanhope: *Man and Microbes*, The Williams & Wilkins Company, Baltimore, 1932.

Buxton, P. A.: *Animal Life in Deserts*, Longmans, Green and Company, New York, 1923.

Carpenter, G. D. H.: *A Naturalist on Lake Victoria*, E. P. Dutton & Company, Inc., New York, 1920.

Carpenter, K. E.: *Life in Inland Waters*, The Macmillan Company, New York, 1928.

Causey, David: *Uninvited Guests: A Short Account of the Animals Living On or In Us*, Alfred A. Knopf, Inc., New York, 1932.

Elton, Charles: *Animal Ecology*, The Macmillan Company, New York, 1927.

Gabrielson, I. N.: *Wildlife Conservation*, The Macmillan Company, New York, 1941.

Gaye, Selina: *The World's Great Farm: Some Account of Nature's Crops and How They Are Grown*, The Macmillan Company, New York, 1900.

Hardy, M. E.: *The Geography of Plants*, Oxford University Press, New York, 1920.

Haviland, Maude D.: *Forest, Steppe, and Tundra*, Cambridge University Press, London, 1926.

Henderson, L. J.: *The Fitness of the Environment*, The Macmillan Company, New York, 1924.

Hesse, R., W. C. Allee, and K. P. Schmidt: *Ecological Animal Geography*, John Wiley & Sons, Inc., New York, 1937.

Johnstone, J.: *Life in the Sea*, Cambridge University Press, London, 1911.

Kellogg, C. E.: *The Soils That Support Us*, The Macmillan Company, New York, 1941.

Leopold, Aldo: *Game Management*, Charles Scribner's Sons, New York, 1937.

Lipman, J. G.: *Bacteria in Relation to Country Life*, 6th ed., The Macmillan Company, New York, 1921.

Shelford, V. E.: *Animal Communities in Temperate America*, University of Chicago Press, Chicago, 1913.

U. S. Department of Agriculture: "Soils and Men," *Yearbook of Agriculture*, 1938, Government Printing Office, 1938.

Weaver, J. E., and F. E. Clements: *Plant Ecology*, McGraw-Hill Book Company, Inc., New York, 1929.

Zinsser, Hans: *Rats, Lice, and History*, Little, Brown & Company, Boston, 1935.

VIII. BIOLOGICAL EXPLORATION, HISTORY, AND PHILOSOPHY

Bates, H. W.: *The Naturalist on the River Amazons*, John Murray, London, 1863; many subsequent editions.

Belt, Thomas: *The Naturalist in Nicaragua*, John Murray, London, 1874; many subsequent editions.

Carpenter, G. D. H.: *A Naturalist on Lake Victoria*, E P. Dutton & Company, Inc., New York, 1920.

Dampier, Sir William: *A History of Science and Its Relations with Philosophy and Religion*, The Macmillan Company, New York, 1940.

Darwin, Charles: *A Naturalist's Voyage: Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H M. S. "Beagle" Round the World*, John Murray, London, 1839; 2d rev. ed., 1845; subsequently reprinted many times.

de Kruif, Paul: *Microbe Hunters*, Harcourt, Brace and Company, New York, 1926.

Fairchild, David: *Exploring for Plants*, The Macmillan Company, New York, 1930.

Smith, Homer W.: *Kamongo*, The Viking Press, New York, 1932.

Wheeler, W. M.: *Foibles of Insects and Men*, Alfred A. Knopf, Inc., New York, 1928.

———: *Demons of the Dust: A Study in Insect Behavior*, W W. Norton & Company, Inc., New York, 1930.

———: *Essays in Philosophical Biology*, Harvard University Press, Cambridge, Mass., 1939.

Zinsser, Hans: *Rats, Lice, and History*, Little, Brown & Company, Boston, 1935.

IX. THE NATURAL HISTORY OF ANIMALS

Allen, A. A.: *The Book of Bird Life*, D. Van Nostrand Company, Inc., New York, 1930.

Anthony, H. E., and others (editors): *Mammals of America*, The University Society, Inc., New York, 1917.

Arnold, A. E.: *The Sea-Beach at Ebb-tide.*, D. Appleton-Century Company, Inc., New York, 1935.

Barbour, Thomas: *Reptiles and Amphibians: Their Habits and Adaptations*, rev. ed., Houghton Mifflin Company, Boston, 1926.

Bassler, R. S., C. E. Resser, W. L. Schmidt, and P. Bartsch: "Shelled Invertebrates of the Past and Present," *Smithsonian Scientific Series*, Vol. 10, 1931.

Borradaile, L. A., and F. A. Potts: *The Invertebrata*, 2d ed., The Macmillan Company, New York, 1935.

Buchsbaum, Ralph: *Animals without Backbones: An Introduction to the Invertebrates*, University of Chicago Press, Chicago, 1938.

Calkins, G. N.: *The Biology of the Protozoa*, Lea & Febiger, Philadelphia, 1926.

———: *The Smallest Living Things*, The University Society, Inc., New York, 1932.

Comstock, J. H., revised by W. J. Gertsch: *The Spider Book*, Doubleday, Doran & Company, Inc., New York, 1940.

Coward, T. A.: *The Migration of Birds*, Cambridge University Press, London, 1912.

Dickerson, M. C.: *The Frog Book*, Doubleday, Doran & Company, Inc., New York, 1906; reprinted, 1920.

Duncan, C. D., and G. Pickwell: *The World of Insects*, McGraw-Hill Book Company, Inc., New York, 1939.

Folsom, J. W., and R. A. Wardle: *Entomology with Special Reference to Its Ecological Aspects*, 4th ed., John Murray, London, and The Blakiston Company, Philadelphia, 1934.

Hamilton, W. J.: *American Mammals*, McGraw-Hill Book Company, Inc., New York, 1939.

Hammerton, J. A. (editor): *Wonders of Animal Life*, 4 vols., W. H. Wise & Company, New York, 1933.

Hegner, R. W.: *Parade of the Animal Kingdom*, The Macmillan Company, New York, 1935.

Hildebrand, S. F., C. W. Gilmore, and D. M. Cochran: "Cold-blooded Vertebrates," Part I, "Fishes"; Parts II and III: "Amphibians and Reptiles," *Smithsonian Scientific Series*, Vol. 8, 1930.

Holland, W. J.: *The Moth Book*, Doubleday, Doran & Company, Inc., New York, 1903; reprinted, 1920.

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Kyle, H. M.: *The Biology of Fishes*, The Macmillan Company, New York, 1926.

Mann, W. M.: "Wild Animals In and Out of the Zoo," *Smithsonian Scientific Series*, Vol. 6, 1930.

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———: *The Book of Birds*, Washington, D. C., 1927.

———: *The Book of Fishes*, Washington, D. C., 1939.

Pearson, T. G., and others (editors): *Birds of America*, Garden City Publishing Company, Inc., New York, 1936.

Pope, C. H.: *Snakes Alive and How They Live*, The Viking Press, New York, 1937.

———: *Turtles of the United States and Canada*, Alfred A. Knopf, Inc., New York, 1939.

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Tate Regan, Charles: *Natural History*, Ward, Lock & Co., Ltd., London, 1936.

Thomson, J. A.: *The Biology of Birds*, The Macmillan Company, New York, 1923.

Ward, H. B., and G. E. Whipple: *Fresh-water Biology*, John Wiley & Sons, Inc., New York, 1918.

Wetmore, A., G. S. Miller, Jr., and J. W. Gridley: "Warm-blooded Vertebrates," Part I, "Birds"; Part II: "Mammals," *Smithsonian Scientific Series*, Vol. 9, 1931.

X. THE NATURAL HISTORY OF PLANTS

Arnold, A. E.: *The Sea-beach at Ebb-tide*, D. Appleton-Century Company, Inc., New York, 1935.

Brown, W H.: *The Plant Kingdom*, Ginn and Company, Boston, 1935.

Calkins, G N.: *The Smallest Living Things*, The University Society, Inc., New York, 1932.

Chase, Agnes, and others (symposium): "Old and New Plant Lore," *Smithsonian Scientific Series*, Vol. 11, 1931.

Clements, F. E., and E. S. Clements: *Flower Families and Ancestors*, The H. W. Wilson Company, New York, 1928.

Gager, C. S.: *The Plant World*, The University Society, Inc., New York, 1933.

Gray, Asa (revised by various authors): *Gray's New Manual of Botany: A Handbook of the Flowering Plants and Ferns of the Central and Northeastern United States and Adjacent Canada*, rev. by B. L. Robinson and M. L. Fernald, American Book Company, New York, many printings. The standard taxonomic work for the northern and eastern states.

Harlow, W. M , and E. S. Harrar: *Textbook of Dendrology*, McGraw-Hill Book Company, Inc., New York, 1937.

Henrici, A. T : *The Biology of Bacteria*, D. C. Heath and Company, Boston, 1934.

House, Homer D.: *Wild Flowers*, The Macmillan Company, New York, 1935.

Hylander, C. J.: *The World of Plant Life*, The Macmillan Company, New York, 1939.

Johnson, A. M.: *Taxonomy of the Flowering Plants*, D. Appleton-Century Company, Inc., New York, 1931

Lutman, B. F.: *Microbiology*, McGraw-Hill Book Company, Inc , New York, 1929.

Marshall, Nina L.: *The Mushroom Book*, Doubleday, Doran & Company, Inc., New York, 1910.

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Robbins, W. W., and F. Ramaley: *Plants Useful to Man*, The Blakiston Company, Philadelphia, 1933.

Small, J. K.: *Manual of the Southeastern Flora*, published by the author, New York, 1933. The standard taxonomic work for the southeastern states.

———: *Ferns of the Southeastern States*, published by the author, Lancaster, Pa., 1938.

Wilson, C. L., and J. M. Haber: *Plant Life*, Henry Holt and Company, Inc., New York, 1935.

APPENDIX C

Glossary

Abiogenesis (ab′ i o jen′ e sis). The origin of living things from nonliving matter; same as spontaneous generation.

absorption (ab sorp′ shun). The taking up of a liquid by osmotic or capillary action.

adjustor neuron. A nerve cell that lies wholly within the central nervous system and intermediates between afferent and efferent neurons.

adrenal gland (ad rē′ nal). One of the endocrine glands that, in man, partially caps the upper end of the kidney. It secretes cortin and adrenalin.

adrenalin (ad rĕn′ al in). One of the hormones secreted by the medulla of the adrenal gland, which produces numerous effects upon the muscular and circulatory systems; also called *epinephrin.*

adrenotropic hormone (a dren′ o trop′ ik). A hormone produced by the anterior lobe of the pituitary body, which stimulates the cortex of the adrenal gland to function.

adsorption (ad sorp′ shun). The adherence of molecules of gases or liquids to the surfaces of solid bodies.

afferent neuron (af′ er ent nu′ ron). A nerve cell that conducts impulses into the central nervous system.

agglutinin (a gloo′ ti nin). An organic substance that causes cells suspended in a liquid to collect into clumps.

albinism. The absence of dark pigments in species that are normally colored; manifested among mammals by white skin and hair and pink iris.

Algae (ăl′ jē). One of the primary divisions of the Thallophyta. The simplest plants, in which the body is a thallus without true roots, stems, or leaves. All algae contain chlorophyll, and most of them are aquatic.

allantois (a lan′ to is). An organ developed by the embryos of those animals producing an amnion. It arises from the posterior portion of the alimentary canal and projects from the body at the umbilicus (marked by the navel of the adult).

alternation of generations. Usually refers to the alternation of a sexual generation with an asexual one; sometimes to the alternation of a bisexual generation with a unisexual (parthenogenetic) one.

alveolus (al vē′ o lus). An expanded air sac terminating the minute branchlets of the bronchial tubes.

amino acid (a mē′ no). One of a number of organic acids containing the NH_2 (ammonium) radical. These acids enter into the composition of all proteins and are produced by the splitting of proteins.

ammonite (ăm′ o nīt). An extinct cephalopod mollusk having a coiled shell and complexly folded sutures.

amnion (am′ ni on). A thin membrane forming a closed sac surrounding the embryos of reptiles, birds, and mammals.

Amoeba (ă mē′ ba). A genus of naked, pseudopod-forming Protozoa, class Rhizopoda.

Amphibia (am fib′ ĭ *a*). A class of vertebrates, intermediate between the fishes and reptiles, including the frogs, toads, newts, salamanders, and their allies.

Amphioxus (ȧm′ fė ok′ sus). The lancelet, a primitive fish-like animal belonging to the phylum Chordata, subphylum Cephalochordata.

Amplexus (am plek′ sus). An embrace; specifically, the sexual embrace of the male toad or frog.

amylopsin (am′ i lop′ sin). A starch-digesting enzyme produced by the pancreas.

analogy. Correspondence in function or in superficial appearance between organs or parts of different origin and basic structure.

anaphase (an′ a faze). That stage of cell division during which the chromosomes pass from the middle to the ends of the spindle.

angiosperm (an′ ji o spurm′). A member of a group of plants in which the seed is formed within an ovary. One of the two major taxonomic subdivisions of the Spermatophyta.

animal pole. In eggs with much yolk, that part in which the protoplasm is concentrated and which in most animals produces the nervous system, sense organs, etc. Other features may also characterize the animal pole

Annelida (a nel′ i da). A phylum of segmented animals typically characterized by having an elongated body composed of segments, an extensive coelom, a double ventral nerve cord, and paired nephridia in some or most of the segments.

annual ring. In the stems of most trees and shrubs, any of the rings seen in cross sections or the layers seen in longitudinal sections, marking the annual growth in diameter and consisting of the alternating zones of spring and summer wood formed by the cambium.

antenna (an ten′ a). A movable, segmented organ of sensation on the heads of insects, myriapods, and crustaceans; a "feeler."

anther (an′ ther). In seed plants, the part of the stamen that develops and contains pollen.

antheridium (an′ ther id′ i um). The male reproductive organ in lower plants, corresponding to the anther of the flowering plants.

anthropoid (an′ thro poid′). Resembling man; applied to Primates of the suborder Anthropoidea, especially to the apes of the family Simiidae, including the gibbons, chimpanzee, orangutan, and gorilla.

antibody (an′ ti bo′ di). An antagonistic or protective substance, produced by the blood, which neutralizes or offsets the injurious effects of foreign proteins.

antigen (an′ ti jen). A protein substance, such as a toxin, enzyme, or any of certain constituents of blood corpuscles or of other cells, which, when introduced into the blood, stimulates the production of an antibody.

antitoxin (an′ ti tok′ sin). An antibody formed in the blood as a result of the introduction of a toxin and capable of neutralizing the specific toxin that stimulated its production.

anus (ā′ nus). The posterior opening of the digestive tract.

aorta (ā or′ ta). The large systemic artery or arteries leading away from the heart.

appendicular skeleton (ap′ en dik′ u lar). In vertebrates, the bones of the limbs and their attaching girdles.

aqueous humor (ak′ wē us hū′ mor). A limpid fluid occupying the space between the crystalline lens and the cornea of the eye.

Arachnida (a rak′ ni da). A class of Arthropoda, comprising the spiders, mites, ticks, scorpions, and their allies.

arachnoid membrane (a rak′ noid). In vertebrates, a thin tissue surrounding the brain and spinal cord between the dura mater and the pia mater. It consists of delicate connective tissue, having the free surfaces covered with endothelium.

archegonium (ar′ ke gō′ ni um). The female reproductive organ in lower plants, analogous to the pistil of flowering plants.

archenteron (ar ken′ ter on). The primitive enteron or digestive sac of the gastrula; the equivalent of the gastrovascular cavity of gastrulalike animals, such as Hydra.

archosaur (ar′ ko sawr). The predominant group of reptiles of the Mesozoic era.

artery (ar′ ter i). A blood vessel conducting the blood away from the heart.

Arthropoda (ar throp′ o da). A phylum consisting of the segmented animals having jointed limbs.

artifact (ar′ tĭ fact). A product of human workmanship, especially one of the simpler products of primitive art or industry, as distinguished from a "natural" object.

Artiodactyla (ar′ ti o dak′ ti la). One of the groups of ungulate mammals, in which the major axis of the foot lies between the third and fourth toes.

ascorbic acid (as cor′ bic). Vitamin C; an acid, with the empirical formula $C_6H_8O_6$, which prevents or cures scurvy.

asexual reproduction. A type of reproduction in which new individuals are produced directly from the somatic tissues of the parent individual.

assimilation (a sim′ i lā′ shun). The conversion or incorporation of nutritive material into the fluid or solid substance of the body.

association neuron. A nerve cell entirely within the central nervous system, which stores, sorts, and relates the impulses that reach the higher nerve centers.

asymmetry (a sim′ met ri). Absence of any kind of symmetry or departure from a strictly symmetrical condition.

auricle (aw′ rĭ kl). The anterior chamber of the heart in fish and either of the two anterior chambers in higher vertebrates.

autogenous variation (aw toj′ e nus). "Self-produced" variation, which is heritable, as opposed to environmentally produced variation, which is not heritable.

autonomic nervous system (aw′ to nom′ ic). In vertebrates, a part of the peripheral nervous system regulating involuntary responses, especially those concerned with nutritive, vascular, and reproductive activities.

autonomic trunk. One of a pair of longitudinal nerve tracts that form a part of the autonomic nervous system. These trunks lie outside the central nervous system and provide a pathway for impulses parallel to but semiindependent of the spinal cord.

autosome (aw′ tō sōm). One of the typical or ordinary chromosomes, as distinguished from the sex chromosomes; normally paired and similar in both sexes.

Aves (ā′ vēz). The class of vertebrates consisting of the birds.

axial skeleton (ak′ si al). That part of the vertebrate skeleton forming the main supporting axis of the body and including the skull, vertebral column, ribs, sternum, and hyoid apparatus.

axil (ak′ sil). The angle formed by a leaf or branch with the stem.

axon (ak′ sŏn). A projection from a nerve cell that normally conducts impulses away from the body of the cell.

Bacillus (bă sil′ us). A large genus of bacteria, characterized by their rod shape.

backcross. A cross between an F_1 individual and one of its parent types. Typically, the mating of the F_1 individual with an individual from the homozygous recessive stock.

Bacteria (bak tēr′ i a). Microscopic one-celled plants, which lack definite nuclei and chlorophyll and reproduce by fission.

bark. That part of the stem of a vascular plant lying outside the woody (xylem) cylinder.

bilateral symmetry. An arrangement of the parts of an object such that the halves on opposite sides of one and only one definite plane are mirrored images of each other. Among bilaterally symmetrical plants and animals minor departures from such perfect symmetry always exist.

bile. A yellow or greenish viscid fluid secreted by the liver, stored in the gall bladder, and discharged into the intestine during digestion, its chief function being the emulsification of fats.

binary fission (bī′ na ri). The division of a unicellular organism into two equal parts. A common method of reproduction in Protozoa and Protophyta.

biota (bī ō′ ta). All the animals and plants of a given area, habitat, or period of time.

biotic potential (bī ot′ ik). The maximum possible reproductive rate of a species.

biovular twins (bī′ ŏv′ u lar). Twins produced from two separate eggs; fraternal twins.

bipolar neuron (bī′ pōl′ ar). A neuron with one axon and one dendrite; for example, the afferent nerves in vertebrates, with their cell bodies in the dorsal-root ganglia.

biradial symmetry (bī rād′ i al). Radial symmetry combined with bilateral symmetry.

biramous (bī rā′ mus). Having, or consisting of, two branches.

bisexual reproduction. A type of reproduction involving the fertilization of an ovum by a spermatozoon.

blastocoele (blas′ tō sēl). The cavity within the blastula.

blastopore (blas′ tō pōr). The opening that connects the archenteron of the gastrula with the exterior.

blastula (blast′ you la). An early developmental stage, in which the embryo consists of a hollow ball of cells.

blue-green algae (ăl′ jē). Algae of a class in which there is a bluish pigment in addition to the green chlorophyll; the Cyanophyceae.

bone. A type of connective tissue consisting of cells separated by a dense, strong matrix, composed chiefly of calcium phosphate.

Bowman's capsule. The expanded end of a kidney tubule, in which a glomerulus is located.

Brachiopoda (bra′ kē op′ o da). A group of marine animals of uncertain rank and relationship. They have a bivalve shell, the valves dissimilar, one covering the dorsal and one the ventral side of the body, and each valve itself bilaterally symmetrical.

bract. The leaf of an inflorescence; specifically, the bract is the small leaf or scale from the axil of which a flower or its pedicel proceeds.

bronchial tube (brong′ ki al). One of the subdivisions of the trachea, or windpipe.

brown algae (ăl′ jē). Algae of a class in which brown pigment masks the green; the Phaeophyceae.

Bryophyta (brī of′ i ta). A phylum of plants comprising the mosses and liverworts.

Bryozoa (brī o zo′ a). A group of marine and fresh-water animals of uncertain rank and relationships; mostly small, colonial, bearing tentacles; commonly known as *moss animals*.

bud. The rudimentary state of a stem or branch; an unexpanded flower.

caecum (sē′ kum). The blind pouch at the beginning of the large intestine; homologous with the vermiform appendix of man.

calciferol (kal sĭ′ fer ōl). A substance produced by activation of the pro-vitamin ergosterol through irradiation by ultra-violet light; apparently the same as vitamin D.

calyx (kāy′ liks). The outer whorl or series of floral leaves.

cambium (kam′ bi um). A soft formative tissue that gives rise to new tissues in the stems and roots of dicotyledonous and gymnospermous shrubs and trees and that consists of a layer of persistently meristematic (embryonic) cells.

canine tooth (kā′ nīn). The pointed tooth next to the incisors.

capillaries (kap′ il lar ēz). Numerous exceedingly minute vessels conveying blood through the tissues from the arteries to the veins, or, in a portal system, from one vein to another.

carbohydrate (kar′ bo hī′ drāt). Any member of a group of neutral compounds composed of carbon, hydrogen, and oxygen, with the latter two elements present in the same relative proportions as in water (two H to one O); the starches, sugars, and related substances.

Carnivora (kar niv′ o ra). An order of mammals, most of which are largely or entirely carnivorous in habits; examples are the wolf, cat, weasel, badger, and raccoon.

carotene (kar′ o tēn). A yellow or orange-yellow organic substance found in the chromoplasts of various plants; the precursor of vitamin A.

cartilage (kar′ ti lij). A flexible, somewhat translucent type of connective tissue composed of cells imbedded in a matrix; found on the ends of bones, at joints, and in other situations. In the young of vertebrates, a forerunner of many of the bones

catabolism (ka tab′ o lizm). The destructive phase of metabolism; the disintegration or breaking down of protoplasm, with liberation of energy.

catalyst (kat′ a list). A substance that brings about or accelerates a chemical reaction but is not consumed in that reaction. It probably often participates in the reaction but is promptly reformed.

Catarrhini (kat′ a rī′ nē). A superfamily of the order Primates, including the Old World apes and monkeys and man, distinguished, in part, by having the nostrils close together, oblique, and directed downward.

catastrophism (ka tas′ tro fizm′). The erroneous hypothesis that there has been a succession of great catastrophies in the geological past, each of which destroyed all the life of the time and was followed by a new creation of different and higher forms of life.

cell. A mass of protoplasm containing a nucleus or nuclear material.

cell membrane. A thin layer of more or less differentiated and semipermeable protoplasm which surrounds a cell, through which all contacts with the external medium are made.

cell products. Nonliving substances produced by cells.

cellulase (sel′ you lās). An enzyme, found in plants, which changes cellulose to glucose.

cell wall. A nonliving structure secreted by a cell around itself. It is commonly composed of cellulose or chitin and is especially characteristic of plant cells. Most animal cells lack cell walls.

central nervous system. In vertebrates, the brain and spinal cord.

centriole (sen′ trē ōl). A minute body sometimes discernible within a centrosome.

centrolecithal egg (sen′ tro les′ i thal). A type of egg characterized by having a comparatively large central core of yolk surrounded by a peripheral layer of cytoplasm; the eggs of insects are typical examples.

centrosome (sen′ tro sōm). A minute protoplasmic body found in the cytoplasm near the nucleus, less often in the nucleus, of many animal and a few plant cells. It takes an important part in mitosis and is regarded by many as the center of the dynamic activity manifested in that process.

centrum (sen′ trum). The massive portion of a vertebra ventral to the neural canal.

cephalization (sef′ ă li zā′ shun). Tendency to domination by the head region in animal life; localization of important functions, organs, or parts in or near the head.

Cephalopoda (sef′ ă lŏp′ o da). A class of Mollusca, comprising the octopods, squids, cuttlefishes, and nautili; animals in which the molluskan foot is developed into a headlike structure with eyes and a circle of arms

cephalothorax (sef′ ă lo thō′ raks). A fused head and thorax, found in crayfishes, spiders, and their allies.

cerebellum (ser′ e bel′ um). A large dorsally projecting part of the brain, anterior to and above the medulla, which it partly overlaps

cerebral hemispheres (ser′ e bral). The anterior (in man, the upper) part of the brain, consisting of two hemispherical masses.

cerebrospinal fluid (ser′ e bro spī′ nal). A lymphlike fluid found in the cavities and canals of the brain and spinal cord and between the membranes that cover them.

cervical (ser′ vi kl). Pertaining to the neck.

cevitamic acid (sē′ vi tam′ ik). A synonym for ascorbic acid, vitamin C.

chlorophyll (klo′ ro fil). The green coloring matter of plants, found in the chloroplasts of cells exposed to light; the essential catalytic agent in the photosynthetic process.

chloroplast (klo′ ro plast). A plastid containing chlorophyll, developed only in cells exposed to light.

Chordata (kor dā′ ta). A phylum of animals having, at least at some stage of development, a more or less well-developed notochord, a dorsally situated hollow central nervous system, and gill clefts in the walls of the pharynx.

chorion (kō′ ri on). A membrane enveloping the fetus of mammals, external to and enclosing the amnion.

choroid coat (kō′ roid). A thin, dark brown membrane lining the inner surface of the sclerotic coat of the eye of vertebrates.

chromatid (krō′ ma tid). One of the four "half-chromosomes" composing a tetrad.

chromatin (krō′ ma tin). The deeply staining substance present in the nucleus of a cell.

chromosome (krō′ mo sōm). One of the rodlike or rounded masses of chromatin that become discernible at the time of cell division.

chyme (kīm). The semifluid mass of partly digested food resulting from the action of the gastric juice and expelled by the stomach into the duodenum.

cilia (sĭl′ i a). Short, hairlike processes, found on many cells, capable of a vibratory or lashing movement.

ciliary muscles (sil′ i ar′ i). A set of involuntary muscles in the eye, extending forward from the region of the ligaments of the lens; their action alters the lens shape, making possible accommodation of the eye to distant or near vision.

circulatory system. The blood and blood vessels; the common carrier that connects each part of the body with all the others.

class. A subdivision of a phylum; a group of higher rank than the order.

clavicle (klav′ i kl). The collarbone in man. One of the bones of the ventral part of the pectoral girdle in vertebrates in general.

cleavage. Division or segmentation of an egg.

climax community. A community or society made up of species that are well adapted for interspecific (biotic) competition in a favorable physical environment; such a community tends to perpetuate itself indefinitely, in contrast to pioneer communities and those of the preclimax succession.

cloaca (klo ā′ ka). A common passageway through which the intestine, kidneys, and sexual organs discharge their products; present in some fishes, in amphibia, reptiles, birds, and a few mammals.

closed vascular bundle. A vascular bundle in which the meristematic tissue is entirely converted into xylem and phloem; characteristic of the monocotyledons.

club mosses. The Lycopodiales, one of the groups of fern allies (Pteridophyta); formerly represented by much larger, more numerous, and more highly differentiated species than exist today.

coccyx (kok′ siks). The end of the vertebral column beyond the sacrum in man and apes; the rudiment of a tail

cochlea (kok′ lē a). The portion of the inner ear containing the auditory sense organs; spiral in form in man and the higher vertebrates.

Coelenterata (sē′ len ter ā′ ta). A phylum of invertebrates in which the members are radially symmetrical and diploblastic and possess a coelenteron, tentacles, and stinging cells in the ectoderm.

coelenteron (sē len′ ter on). The gastrovascular cavity in forms like Hydra and other coelenterates, which have only one body cavity. It serves the digestive and circulatory functions and has only one opening, the mouth.

coelom (sē′ lōm). The true body cavity; a cavity within the mesoderm, on the walls of which the principal reproductive organs are located.

collenchyma (ko leng′ ki ma). In higher plants, a supporting tissue composed of living cells, usually elongated, with the walls variously thickened, especially at the angles, but remaining capable of further growth.

colloid (kol′ loid). A mixture in which particles, invisible through a microscope but greater in size than molecules, are held in suspension in a liquid

commensal (ko men′ sal). Not truly parasitic but living in, with, or on another organism, and usually partaking of the same food.

communicating neurons. Nerve cells located entirely within the central nervous system, which provide for many types of connections between its various parts and levels.

complementary genes. Two sets of genes, neither alone producing a visible effect but together producing such an effect.

complete flower. A flower possessing all the typical parts—pistil(s), stamens, petals, and sepals.

condyle (kon′ dīl). An articular prominence on a bone which fits into a corresponding socket on another bone

cones. Together with the rods, these constitute the sensitive elements of the retina, where, by photic (light) stimulation, the visual impulses are generated. Stimulation of the cones results in perception of color.

conjugation (kon′ jŭ gā′ shun). The fusion of or temporary union between two unicellular organisms, involving a fusion of their nuclei or an interchange of nuclear material; followed by fission into daughter cells.

connective tissue. A tissue, composed of cells and certain other materials produced by the cells, which in its simple form binds organs and other tissues together.

In a broad sense, it includes such modified tissues as cartilage, bone, tendon, and ligament.

contractile vacuole (vak′ u ōl). A vacuole whose contents are periodically ejected to the outside of the cell.

convergent evolution. The tendency for two separate stocks of organisms to give rise to structures that are superficially similar, or to become similarly adapted to life in similar habitats.

coprolite (kop′ ro līt). Fossil dung or excrement.

cork cambium (kam′ bi um). In plants, a layer of meristematic tissue arising in certain zones of the cortex or rarely in the epidermis, and producing an impermeable layer of cork cells.

cornea (kor′ nē a). The transparent bulging membrane in front of the pupil of the eye.

corolla (ko rol′ a). The petals of a flower collectively.

corpus luteum (kor′ pus lu′ tē um). A yellowish mass of cells invading the space in an ovary from which an ovum has escaped; it functions as an endocrine gland, producing the hormone progestin.

cortex (kor′ teks). The outer layer of various structures. In plants, those parts of the axis outside the stele. In animals, the layer of gray matter that covers the cerebrum and dips into its folds. The enlarged cerebral cortex of mammals is called the *neopallium.*

cortin (kor′ tin). The hormone produced by the cortex of the adrenal glands.

cotyledon (kot i lē′ dun). The first leaf, or one of the first pairs or whorls of leaves, developed by the embryo sporophyte in seed plants.

cotylosaur (kot′ i lo sawr). A member of an order of reptiles of the late Paleozoic and early Triassic, comprising the most primitive of reptiles, which had short legs, massive bodies, and solidly roofed skulls.

Cowper,s glands. Two small glands discharging into the male urethra in smammal.

cranial nerve. One of the 10 or 12 pairs of nerves arising from the central nervous system within the skull.

cranium (krā′ ni um). The skull or brain case.

Creodonta (krē′ o don′ ta). A suborder of primitive mammals (order Carnivora), ancestral to the fissipedes but showing relationship to the primitive ungulates. The flesh-toothed mammals.

crossing over. An interchanging of genes between parts of homologous chromosomes, believed to occur during synapsis.

cross-pollination. The deposition of pollen from one flower on the stigma of another.

Crustacea (krus tā′ shē a). A class of arthropods including the lobsters, crabs, water fleas, barnacles, etc.

crystalline lens. A transparent, refractive body, with convex anterior and posterior surfaces, in the eyes of vertebrates.

culture. The sum of the activities of a people, as shown by their industries and other discoverable characteristics.

cursorial (kur so′ ri al). Adapted to running or fast walking and not to grasping—for example, the limbs of a horse.

cuticle (kū′ ti kl). In plants, a very thin, detachable skin; it is formed from the cutinized outer walls of the younger epidermal cells. In animals, an external membranous or hardened noncellular investment secreted by the cells of the epidermis or by the outer surface of the body.

cutin (kū′ tin). In plants, a waxlike, impermeable material secreted by the epidermal cells.

cytolysin (sī tol′ i sin). A substance causing dissolution or disintegration of cells.

cytoplasm (sī′ to plazm). The protoplasm of a cell, exclusive of the nucleus.

deciduous (de sid′ you us). Falling off or shed at maturity or at certain seasons.

dendrite (den′ drīte). A projection from a nerve cell that normally conducts impulses toward the body of the cell.

dentary (den′ ta ri). A bone of the distal part of the lower jaw of many vertebrates; the only bone of the jaw in mammals.

dermis (der′ mis). The inner layer of the skin.

diabetogenic hormone (dī a bē′ to jen′ ik). One of the hormones, produced by the anterior lobe of the pituitary body, which aids in regulating the use of carbohydrates and fats in the body and probably opposes the action of insulin.

diaphragm (dī′ a fram). A partition; specifically, the muscular partition between the thorax and abdomen of a mammal.

diastase (dī′ a stās). An enzyme found in plants that changes starch to maltose.

dicotyledon (di′ kot i lē′ dun). A plant having two cotyledons or seed leaves; a member of one of the two primary divisions of the angiosperms

diencephalon (dī′ en sef′ a lon). The second of the five major divisions of the vertebrate brain, lying posterior to the telencephalon and including the optic thalami, optic tracts, and pineal and pituitary bodies.

diffusion (dif fū′ zhun). The spreading of the molecules of one substance among those of another.

digestive system. A system of organs that renders food absorbable by dissolving it and breaking it down into simpler chemical compounds, chiefly through the action of secretions containing enzymes.

dinosaur (dī′ no sawr). A member of either of two orders (Saurischia and Ornithischia) of extinct reptiles of Mesozoic time; many were of large size.

dioecious (dī ē′ shus). A species having male reproductive organs in one individual, female organs in another.

diploblastic (dip′ lo blas′ tik). Having two germ layers.

diploid (dip′ loid). Double; specifically, the double ($2n$) number of chromosomes found in the somatic cells and in germ cells before meiosis, in animals, and in all the cells of the sporophyte generation of plants.

Dipnoi (dip′ noy). A group of remarkable fishes that have, in addition to gills functioning in the usual manner, a lung or pair of lungs communicating with the ventral side of the esophagus by a short tube; the lungfish.

disaccharide (di sak′ a rīd). Any of a group of sugars that on hydrolysis yield two monosaccharide molecules.

dorsal. Pertaining to the back; hence usually upper; in the trunk of the human body, posterior.

dorsal ramus (dor′ sal rā′ mus). That branch of a spinal nerve which supplies the skin and muscles of the back.

dorsal root. The dorsal one of the two roots by which a spinal nerve is connected with the spinal cord; its fibers are afferent and largely sensory in function, and their cell bodies are located in the dorsal-root ganglion.

dorsal-root ganglion. An enlargement in the dorsal root of a spinal nerve, in which the cell bodies of the afferent neurons are located.

"double fertilization." In plants, a form of fertilization, characteristic of angiosperms, in which the egg nucleus is fertilized by one sperm nucleus (true fertilization) and the double nucleus of the endosperm (consisting of the polar nuclei) by another; the endosperm tissues are therefore furnished with a triploid chromosome complement.

ductless gland (dukt′ les). An endocrine gland, with no efferent duct, its secretion being poured directly into the blood or lymph.

duodenum (du′ o dē′ num). The first of the three divisions of the small intestine.

dura mater (du′ ra mā′ ter). The tough, fibrous membrane, lined with endothelium on the inner surface, which forms the outermost envelope of the brain and spinal cord; it encloses the arachnoid membrane and pia mater.

dyad (dī′ ad). In meiosis, a double body formed by the division of a tetrad into two parts. It consists of two "half chromosomes" or chromatids—either two halves of the same chromosome, or one half-chromosome from each of the two homologous chromosomes that produced the tetrad by synapsis.

ecesis (ĕ sē′ sis). The establishment of a migrant in a new habitat.

Echinodermata (ĕ kī′ no der′ ma ta). A phylum of marine animals consisting of the starfishes, sea urchins, and their allies. Characterized by radial symmetry, a calcareous skeleton of plates imbedded in the skin, and a water vascular system.

ecology (ĕ kol′ o ji). That branch of biology dealing with the relations of animals or plants to their environment.

ectoderm (ek′ tō derm). One of the primary germ layers. The outer layer of cells of a gastrula or the tissues developed from this layer in later stages, including nervous tissue and the outer epithelial tissues.

ectoparasite (ek′ tō par′ a sīt). Any parasite that lives on the exterior of animals or plants.

ectoplasm (ek′ to plazm). The outer portion of the cytoplasm.

effectors (e fek′ tors). The responding organs, *i.e.*, the muscles and glands.

efferent neuron (ef′ er ent nū′ ron). A nerve cell that carries impulses out of the central nervous system.

Elasmobranchii (ĕ las′ mo brang′ kē ī. A class of fish-like Vertebrata comprising the sharks, skates, rays, torpedoes, and chimeras; the skeleton is cartilaginous.

embryo (em′ bri o). An undeveloped animal still in the egg membrane or in the maternal uterus, or the young sporophyte plant contained in the seed.

embryology (em bri ol′ o jē). The science that deals with the development of the embryos, or young stages, of plants or animals.

emulsion (ē mul′ shun). A suspension of fine particles or globules of one liquid in another.

endocarp (en′ dō karp). The innermost layer of the matured ovary wall in fruits.

endocrine (en′ dō krīn). Secreting internally; applied especially to glands whose secretions pass directly into the blood or lymph.

endocrine system. A set of glandular organs that plays an important part in the regulation and coordination of the body functions by means of hormones.

endodermis (en′ dō der′ mis). In vascular plants, a single layer of living cells, with variously but characteristically thickened walls and no intercellular spaces, which surrounds the vascular tissues, lying between the pericycle and cortex and occurring in nearly all roots and in certain stems and leaves.

endoparasite (en′ dō par′ a sīt). Any parasite that lives internally in an animal or plant.

endoplasm (en′ dō plazm). The inner or central portion of the cytoplasm of the cell.

endosperm (en′ dō sperm). The nutritive tissue formed within the embryo sac in seed plants; see *double fertilization.*

enterokinase (en′ ter o kī′ nās). The ferment (enzyme) that transforms trypsinogen into trypsin.

enteron (en′ ter on). A digestive tube open at both ends, *i.e.*, having both a mouth and an anus.

entoderm (en′ tō derm). One of the primary germ layers. The inner layer of cells of a gastrula or the tissues that develop from this layer in later stages; including the inner layer of the digestive tract and of the glands and organs that open into it.

enzyme (en′ zīm). An organic catalytic substance that brings about a chemical reaction but is not consumed by that reaction. It probably participates in the reaction but is promptly restored.

epidermis (ep′ i der′ mis). The outer of the principal layers of the vertebrate skin. Also, an outer covering layer of cells in general.

epididymis (ep′ i did′ i mis). An elongated mass at the back of the testicle, composed chiefly of the greatly convoluted efferent tubules of that organ.

epiglottis (ep′ i glot′ is). A fibrous, cartilaginous lid at the base of the tongue; the larynx, at the time of swallowing, is raised to press against this lid, thus closing the air passage to the lungs.

epinephrin (ep′ i nef′ rin). Another name for adrenalin, the hormone produced by the medulla of the adrenal glands.

epithelial tissue (ep′ i thē′ li al). A cellular tissue covering a free surface or lining a tube or cavity, consisting of one or more layers of cells.

epoch. In geology, a subdivision of a geological period of time.

equatorial plate. The flattened group of chromosomes on the middle of the spindle of a dividing cell, just preceding and during the metaphase.

equation division. One of the divisions occurring during meiosis, in which the two halves of each of the original chromosomes that paired to form a tetrad are separated and go to different daughter cells. Except in details, this division is essentially like an ordinary mitotic division, with quantitatively and qualitatively equal division of the chromatin of each chromosome.

era. One of the major divisions of geologic time.

erepsin (ĕ rep′ sin). A protein-splitting enzyme produced in the small intestine.

ergosterol (er gos′ ter ol). A substance, chemically a solid alcohol, which, when irradiated with ultraviolet light, changes to a substance called *calciferol*. The latter has strong antirachitic (rickets-preventing) properties, and is probably identical with vitamin D. Ergosterol was first isolated from the fungus ergot, whence the name, but is widely present in plant and animal cells.

esophagus, oesophagus, (ĕ sŏf′ a gus). In vertebrates, the passage between the pharynx and the stomach. In the earthworm, a narrow passage leading from the pharynx to the crop.

eugenics (ū jen′ iks). The science that deals with influences that improve inborn or hereditary qualities in a series of generations of a race or breed, primarily those influences admitting of social control. Especially applied to the human race.

Euglena (ū glē′ na). A genus of elongated, flagellated, unicellular fresh-water organisms that contain chlorophyll.

eurypterid (ū′ rip ter′ id). A member of an exclusively Paleozoic order of aquatic arthropods, related to the arachnids and especially to the king crabs and scorpions.

Eustachian tube (ū stā′ kĭ an). A passage between the pharynx and the middle ear.

excretory system. A system of organs specialized for the removal of nitrogenous wastes, certain salts, and a part of the excess body water.

exocarp (ek′ sō karp). In fruits, the outermost layer of the matured ovary wall.

exoskeleton (ek′ so skel′ e tun). A supporting or protective structure developed on or secreted by the outside of the body, as the shell of a crustacean or the chitinous covering of an insect.

external fertilization. Fertilization of the ovum outside the body of the female.

external respiration. The passage of oxygen from the surrounding air or water to the blood.

extracellular digestion. Digestion within a body cavity surrounded by digestive cells.

extra-embryonic membrane (eks′ tră em′ bri on′ ik). A protective membrane formed around the embryo.

family. A taxonomic group of higher rank than the genus but of lower rank than the order.

fat. A compound of glycerol and one or more fatty acids; composed of carbon, hydrogen, and oxygen but with proportionately less oxygen than in carbohydrates.

femur (fē′ mur). The proximal bone of the hind limb; the thighbone.

fetus, foetus (fē′ tus). The young or embryo of a vertebrate animal in the uterus or in the egg; commonly restricted to the young in the later stages of development in the uterus or in the egg.

fibrin (fī′ brin). The insoluble protein formed from fibrinogen during coagulation of the blood.

fibrinogen (fī brin′ o jen). A soluble protein in the plasma that is transformed into fibrin when the blood is shed, causing the blood to clot.

fibrous root system. A root system that is formed from numerous adventitious roots, which develop from the base of the stem or from other parts of the plant.

filament. In flowering plants, the anther-bearing stalk of the stamen.

fission (fish′ un). Reproduction by spontaneous division of the body into two or more parts, each of which grows into a complete organism.

flagellum (flă jel′ um). A long, whiplike propulsory process of a cell.

flame cell. A cell, having a hollow interior in which a tuft of vibratile cilia is located, forming part of a protonephridium.

flower. A special reproductive structure developed only among the angiosperms. Essentially, the flower is a modified leaf-bearing twig, in which some of the parts have been transformed into reproductive organs and others into accessory structures.

follicle (fol′ ĭ kl). A small cavity, or deep, narrow-mouthed depression; specifically, one of the liquid-filled spaces that develop around maturing eggs in the ovary of vertebrates.

food. In animals, usually used to include all the essential materials taken into the digestive system, including proteins, carbohydrates, and fats and also water, a considerable list of inorganic salts and the vitamins; in plants, strictly speaking, the sugar produced by photosynthesis but often used to include the raw materials taken in for food manufacture.

food vacuole (vak′ ū ōl). A digestive space that is temporarily formed within the cell, in Protozoa, sponges, and other lower invertebrates, food particles are taken into the cell and are digested within this space.

foramen magnum (fo rā′ men mag′ num). The large opening in the occipital bone through which the spinal cord passes to become the medulla oblongata.

fossil (fos′ il). Any remains or traces of an animal or plant of past geological ages that have been preserved in the earth's crust.

fovea (fō′ vē a). A small area of the retina where, in daylight vision, the power of discriminating details is the greatest.

fraternal twins. Individuals produced from separate ova. See *biovular twins.*

fruit. A fruit consists of the matured ovary of a flower (including its one or more seeds) and any part of the flower that may be closely associated with the matured ovary.

fungus. A thallophyte that lacks chlorophyll and is saprophytic, parasitic, or symbiotic with green plants; examples are molds, mildews, smuts, ring-worms, mushrooms, etc.

gall bladder. A pouch in which the bile secreted by the liver is stored and concentrated; it connects with the duodenum by way of the common bile duct.

gamete (gam′ ēt). A matured sex cell or germ cell; a minute, nucleated protoplasmic reproductive body (usually an egg or spermatozoon), normally with the haploid chromosome number, capable of uniting with another of like origin to form a new individual.

gametic purity (ga mĕt′ ik). The principle stated in Mendel's first law that a gamete can carry but one of any two alternative characters and hence can never be hybrid.

gametophyte (ga mē′ tō fīt′). In plants showing alternation of generations, the individual or generation that is composed of cells with the haploid chromosome number and that produces gametes.

ganglion (gang′ glĭ on). A mass of nerve-cell bodies, usually forming a thickening in the course of a nerve.

gastrovascular system (gas′ tro vas′ kū lar). A system that functions both as a digestive and a circulatory system, such as the branched digestive tract ramifying through the body of the flatworm Planaria.

gastrula (gas′ troo la). An early developmental stage, formed from a blastula, commonly by the invagination of the vegetative pole of the latter. The gastrula consists of two layers of cells (the outer ectoderm and the inner entoderm) surrounding a cavity (the blastocoele), which communicates with the exterior by means of the blastopore.

genus (jē′ nus), plural, **genera.** A group of species having so many structural features alike that they must be regarded as having sprung from common ancestry; a category of lower rank than the family.

germ cell. A cell capable of reproduction or of sharing in reproduction, as contrasted with the somatic or body cells that are sterile. See *gamete*.

germination (jur′ mĭ nā′ shun). The act of beginning to grow or develop; sprouting.

gland. An organ whose function is the secretion of something to be used in, or ejected from, the body.

glenoid fossa (glē′ noid fŏs′ sa). A smooth, shallow depression in the scapula to receive the head of the humerus.

glomerulus (glo mer′ ū lus). A cluster of blood capillaries within the Bowman's capsule at the end of each tubule in the kidney of a vertebrate animal.

glucose (gloo′ kōs). A monosaccharide with the chemical formula $C_6H_{12}O_6$; dextrose or grape sugar.

glycogen (glī′ ko jen). Animal starch; carbohydrate foods are commonly stored in this form in animal tissues.

gonad (gō′ nad). An animal organ in which germ cells (either oögonia or spermatogonia) are produced or lodged.

gonadotropic hormones (gō′ nad o trop′ ik). Hormones, secreted by the anterior lobe of the pituitary body, which govern or influence the development of sexual maturity, and in the mature animal exhibit a reciprocal relation with the sex hormones that accounts for the sexual rhythms.

goniatite (gō′ ni a tīt′). An extinct cephalopod mollusk having a coiled shell and simply bent or angular sutures.

graptolite (grap′ tō līt′). A fossil hydrozoan coelenterate found from the Upper Cambrian through the Devonian but most abundant in and characteristic of the Ordovician.

gray matter. Nerve tissue consisting largely of nerve-cell bodies and nonmyelinated fibers.

green algae (ăl′ jē). Algae of green or yellow-green color, in which the green of chlorophyll is not characteristically obscured by other pigments; the Chlorophyceae.

growing point. The undifferentiated end of a shoot or vegetative axis (stem or root), consisting of a single cell or more often of a group of cells constituting the primary meristematic tissue.

guard cell. In plants, one of a pair of specialized epidermal cells which together enclose a stoma or opening into the airspaces in the parenchyma.

gymnosperm (jim′ nō spurm). That one of the two classes of Spermatophyta in which the seeds are naked or are not enclosed in an ovary. This class is of lower phylogenetic rank than the other, the flowering plants or angiosperms, in which the seeds are enclosed in an ovary.

hemoglobin (hē′ mo glō′ bin). A reddish protein contained in the red blood cells, having an especial affinity for oxygen

hemophilia (hē′ mo fil′ i a). A condition, usually hereditary, characterized by a tendency to profuse and uncontrollable hemorrhage from even the slightest wounds.

hair follicle (fol′ ĭ kl). A tubular sheath formed by the downward extension of the epidermis, in which the root of a hair is located.

haploid (hap′ loid). Single; referring to the reduced (*n*) number of chromosomes present in the mature germ cells of bisexual animals and in all the cells of the gametophyte generation of plants.

heartwood. The hard central part of the trunk of a tree, consisting chiefly of xylem tissues that no longer function as part of the vascular system, having been filled with resin and tannin; these dead tissues are useful to the plant chiefly on account of their mechanical strength.

hepatic portal vein (hĕ păt′ ik). A blood vessel bringing the blood from the intestine into the liver, where it terminates in a capillary network; the only portal system in man and other higher vertebrates.

herb (erb). A seed plant which does not develop persistent woody tissue, such as that of a tree or shrub, but which is more or less soft or succulent.

herbivorous (her biv′ o rus). Feeding upon plants.

heredity. The passing from generation to generation of qualities common to all members of the race and of such additional qualities as are common to all the members of any given parent-offspring sequence within that race.

hermaphrodite (her maf′ ro dīt′). An individual having both male and female reproductive organs.

hexuronic acid (hex′ ur on′ ik). A synonym for vitamin C (cevitamic acid, ascorbic acid).

Hominidae (hō min′ i dē). The family of mammals to which belong the genera Pithecanthropus, Sinanthropus, Eoanthropus, and Homo, or mankind.

homolecithal (hō′ mō les′ i thal). A type of egg in which the yolk is uniformly distributed throughout and small in amount.

homology (ho mol′ o gi). Similarly of origin in evolution; structures occurring in different organisms that are of similar origin, built on the same fundamental plan.

hormone (hor′ mōn). A substance secreted by an endocrine gland that stimulates activity in an organ by chemical means.

horsetail. A member of one of the groups (Equisetales) of fern allies (pteridophytes), which was formerly represented by much larger and more numerous species than exist today. There is only a single living genus, Equisetum.

humerus (hū′ mer us). The bone of the upper part of the arm or forelimb, from the shoulder to the elbow.

Hydra (hī′ dra). A small, tubular fresh-water animal with tentacles and stinging organs, belonging to the phylum Coelenterata.

hydrolysis (hī drol′ i sis). A chemical process of decomposition involving the addition of water.

hypocotyl (hī′ po kot′ il). In the embryo of a seed plant, that portion of the stem below the cotyledons.

hypothesis (hī poth′ e sis). A proposition, condition, or principle that is assumed, perhaps without belief, in order to draw out its logical consequences and by this method to test its accord with facts that are known or that may be determined.

ichthyosaur (ik′ thi o sawr′). One of the Mesozoic marine reptiles of the group Parapsida, having a fish-shaped body, porpoiselike snout, short neck, and dorsal and caudal fins.

identical twins. See *uniovular twins.*

ilium (il′ i um). The dorsal and upper one of the three bones that make up each lateral half of the pelvis.

immunity. The state or power of resisting the development of a disease or the effects of a toxic agent; used especially in reference to a resistance to infecting microorganisms or their products.

imperfect flower. A flower lacking one or both of the essential parts (stamens and pistil).

incisor tooth (in sī′ sor). One of the anterior teeth, adapted for cutting or clipping off morsels of food. Man has two pairs of upper and two pairs of lower incisors, bordered by the canines.

incomplete flower. A flower lacking any of the full complement of parts (pistil, stamens, petals, sepals).

incus (ing′ kus). The middle one of the chain of three small bones in the ear of mammals.

independent assortment. The principle, stated in Mendel's second law, that when more than one pair of allelomorphic genes are involved in a cross, each pair assorts independently of the others; see *linkage.*

industry. In archeology, an assemblage of artifacts at a given locality and of the same age.

Insecta. The insects; a class of Arthropoda having one pair of antennae, three pairs of legs, and tracheae for respiration; wings are usually present in members of the higher groups.

insertion. The end or part of a muscle by which it is attached to the part to be moved; *cf. origin.*

insulin (in′ su lin). A hormone, produced in the pancreas, essential for the conversion of monosaccharides of the blood into glycogen.

integumentary system (in teg′ u men′ ta ri). That portion of the body which serves as a body covering, for protection, for heat regulation, and for reception of stimuli; the skin.

internal respiration. The transfer of oxygen from the blood to the surrounding cells and of carbon dioxide from the cells to the blood; true respiration.

internode (in′ ter node). The portion of a plant stem between two nodes and destitute of leaves, branches or buds; *cf. node.*

intracellular digestion. Digestion that takes place in a food vacuole within a cell.

invagination (in vaj′ i nā′ shun). An infolding such that an outer surface becomes an inner surface. One portion of a hollow organ drawn back within another portion.

invertase (in ver′ tās). An enzyme capable of splitting cane sugar into glucose and fructose.

iris (eye′ ris). The pigmented diaphragm directly in front of the lens of the eye.

irregular flower. A flower showing inequality in the size, form, or union of its similar parts.

irritability. The power of protoplasm to respond to stimulation.

ischium (is′ ki um). The dorsal and posterior one of the three principal bones composing each half of the pelvis.

isogametes (ī′ so gā′ mēts). Gametes that are not differentiated into smaller (male) and larger (female) but are all alike. This primitive type of reproductive cell is found in certain of the algae.

kidney. The chief organ for the excretion of nitrogenous wastes in most vertebrates; also, an excretory organ in certain other animals.

kinesthetic (kin′ ĕs thet′ ik). The muscle sense; the sensation by which we judge of the position and movement of the head, limbs, and body.

kingdom. One of the two grand divisions, or primary groups, into which living things are classified—the plant and animal kingdoms.

lactase (lak′ tās). An enzyme that splits lactose into glucose and galactose.

lactic acid (lak′ tik). An acid formed from carbohydrates, as in the souring of milk, having the formula $C_3H_3O_6$.

lactose (lak′ tōs). Milk sugar, a disaccharide present in milk, composed of one molecule of glucose and one of galactose; slightly sweet, and less soluble in water than glucose or cane sugar.

Lamarckianism (la mark′ i an ism). The theory of organic evolution proposed by the French naturalist Lamarck that changes in environment cause changes in the structure of animals and plants and that such acquired characters are transmitted to offspring.

larva. The early form of any animal that, while immature, is unlike its parents and must pass through a more or less profound metamorphosis before assuming the adult characters.

larynx (lar′ inks). The voice box, containing the vocal cords and forming the uppermost portion of the trachea.

latent heat. The amount of heat required to change water from its solid state to a fluid state and from a fluid state to a gaseous state without change in its temperature.

leaf. An expanded, lateral outgrowth of the stem, arising at a node and having a bud in its axil.

legume (leg yūm′). A pod; the fruit of plants of the pea family; by extension, a plant of this family (Leguminaceae).

lemur (lē mur). Any of numerous arboreal, chiefly nocturnal mammals, allied to the monkeys but usually regarded as constituting a distinct suborder, Lemuroidea.

Lepidodendron (lep′ i do den′ dron). An extinct arborescent lycopod that flourished during the late Paleozoic; a scale tree, so called because the leaf bases formed a scalelike pattern covering the trunk and branches.

lethal character (lē′ thal). A recessive genetic factor that is lethal in the homozygous condition, bringing about the early death of the individual.

lichen (lī′ ken). A thallophyte in which the plant body is made up of a fungus growing in intimate symbiotic relationship with an alga.

ligament (lig′ a ment). A tough, fibrous band of tissue that connects bones or supports visceral organs.

lignin (lig′ nin). A substance or mixture of substances related physiologically to cellulose and with it constituting the essential part of woody tissue.

linin (lī′ nin). The substance of the fine network within the nucleus of a resting cell, upon which the chromatin is located.

linkage. The occurrence of two or more genes in the same chromosome as a result of which they tend to remain together in gametogenesis, instead of showing independent assortment.

lipase (lip′ ās). A fat-splitting enzyme.

liverwort. A member of the Hepaticae, one of the two large groups into which the plant phylum Bryophyta is divided.

lumbar. Pertaining to the loins, the region of the back caudad of the ribs.

lungfish. Any fish of the subclass Dipnoi, so called because they breathe by lungs as well as gills.

lymph (limf). A colorless, alkaline, nutritive fluid in animal tissue, formed from blood and draining into the circulatory system.

lymphatic system (lim făt′ ik). A secondary circulatory system that returns the lymph to the blood-system proper.

lymph node. One of the rounded masses of lymphoid tissue, surrounded by a capsule of connective tissue, that occur in various parts of the body in the course of the lymphatic system.

macrogamete (mak′ ro gă′ mēt). One of the larger, nonmotile, egglike female reproductive cells of most thallophytes and of other plants having sexual reproduction; *cf microgamete, isogametes.*

macrospore (mak′ ro spōr). In spermatophytes and some pteridophytes, in which spores of two sizes are produced, the larger type of spore, from which the female gametophyte generation develops, *cf. microspore*

malleus (mal′ i us). The outermost of the chain of three small bones in the middle ear of mammals.

Malphigian corpuscle (mahl pē′ ji an kor′ pus sl). One of the numerous excretory bodies in the kidneys of vertebrate animals, each composed of the expanded end of a kidney tubule (Bowman's capsule) and an enclosed knot of blood capillaries (glomerulus).

Malphigian layer (mahl pē′ ji an). The deeper portion of the epidermis of the skin, consisting of cells whose protoplasm has not yet changed into horny material.

maltase (mal′ tās). An enzyme splitting maltose into glucose.

maltose (mal′ tōs). A disaccharide sugar, the end product of hydrolysis of starch in the presence of diastase.

Mammalia (ma mā′ li a). A class of vertebrates having hairy bodies, producing young within the body of the mother, and nourishing the young after birth with milk secreted by the mother.

mammary gland (mam′ a ri). One of the two or more large compound glands, characteristic of the mammals, which, in the female, secrete milk for the nourishment of the young.

mandible (man′ di bl). The lower jaw of vertebrates.

Marsupialia (mar′ soo pi ā′ li a). An order of mammals characterized by having a pouch in which the young, born in a very immature state, are carried (for example, the kangaroo and the opossum).

Mastodon (mas′ tō don). An extinct genus of elephantlike animals of Pliocene and Pleistocene times.

matrix (mā′ triks). The nonliving intercellular substance of a tissue, secreted by the cells.

maturation (mat′ ū rā′ shun). Becoming mature; as applied to germ cells, a process undergone before they become functional, consisting essentially of two cell divisions, in one of which the paired chromosomes separate to form two nuclei, each with only a single (haploid) set of chromosomes.

maxilla (mak sil′ a). A bone of the upper jaw.

medulla (me dŭl′ a). The deep or inner substance or tissue of an organ or part, as of the kidney.

medulla oblongata (me dŭl′ a ob lon gā′ ta). The afterbrain or myelencephalon, lying between the spinal cord and the metencephalon (cerebellum and pons).

medusa (me dū sa). A jellyfish; the adult stage of all scyphozoan coelenterates and the free-swimming individuals of the sexual generation of many hydroid species.

meiosis (mī ō′ sis). Separation of maternal from paternal chromosomes in oogenesis or spermatogenesis; *cf. maturation*

menstruation (men stroo ā′ shun). A periodic flow of blood or bloody fluid from the uterus, occurring normally (in the human species) once every four weeks and lasting typically 3 to 5 days; see the table on page 125.

meristem (mār′ ĭ stem). In plants, an embryonic or undifferentiated tissue the cells of which are capable of active division and from which the differentiated tissues of the plant develop.

mesencephalon (mes en sef′ a lon). The midbrain of vertebrates; the third of the five major divisions of the brain, lying between the diencephalon and the metencephalon and including the optic lobes

mesocarp (mes′ o karp). In fruits, the middle layer of the matured ovary wall.

mesoderm (mes′ o derm). The middle one of the three primary germ layers from which the various tissues of the animal body are derived The chief tissues developed from mesoderm are three in number, namely, sustentative, muscular, and vascular.

mesoglea (mes o glē′ a). In diploblastic animals (sponges and coelenterates), a gelatinous, mostly noncellular layer between the entoderm and ectoderm. If cells are present they are not mesodermal in character.

mesophyll (mes′ o fil). The green parenchyma between the upper and lower epidermal layers of a foliage leaf.

metabolism (me tab′ o lizm). The sum total of the physical and chemical processes going on in protoplasm.

metagenesis (met′ a jen′ e sis). The regular alternation of sexually and asexually produced generations that occurs in most coelenterates and in certain other animals.

metamerism (me tam′ er izm). The condition of being divided into a linear series of similar segments or somites; characteristic of the bodies of annelids, arthropods, and chordates.

metaphase (met′ a fāz). That stage of cell division in which the chromosomes lie in the equatorial plate and during which equal splitting of the chromosomes to form two sets of daughter chromosomes becomes evident.

metatarsal (met a tar′ sal). One of the bones forming the body of the (hind) foot of vertebrates.

Metazoa (met a zō′ a). A group comprising all animals except Protozoa. Although the term contrasts the multicellular animals with Protozoa, it is not the name of any taxonomic group.

metencephalon (met′ en cef′ a lon). The fourth of the five major divisions of the vertebrate brain, lying between the mesencephalon and the myelencephalon and including the cerebellum and pons.

microgamete (mī′ kro gă′ mēt). One of the smaller, more motile, spermlike male reproductive cells of most Thallophyta and other plants having sexual reproduction; *cf. isogametes, macrogamete.*

microspore (mī′ kro spōr). In spermatophytes and some pteridophytes, in which spores of two sizes are produced, the smaller type of spore, from which the male gametophyte generation develops; *cf. macrospore.*

microtome (mī′ kro tōm). An instrument for cutting thin sections, as of organic tissues, for microscopic examination by transmitted light.

middle ear. A cavity connected with the pharynx by the Eustachian tube, separated from the external auditory canal by the tympanic membrane, containing a chain of three small bones that connect this membrane with the internal ear.

millipede (mil′ ĭ pēd). An arthropod belonging to the class Myriapoda. Body more or less cylindrical, covered with a hard integument and composed of numerous segments; distinguished from centipedes by lacking poison "jaws" and by having most of the segments fused in pairs, so that most of the apparent segments bear two instead of a single pair of appendages.

mitosis (mĭ tō′ sis). Normal cell division, involving the formation of chromosomes, spindle fibers, etc., and the longitudinal splitting of each chromosome into two daughter chromosomes, one of which goes to each of the two daughter cells.

modifying gene. A gene which does not produce any visible effect by itself but which does modify the phenotypic expression of some other, nonallelomorphic gene.

molar tooth. A mammalian tooth in the posterior portion of the jaws, having a broad rounded or flattened surface adapted for grinding food.

Mollusca (mo lŭs′ ka). The phylum of animals that includes the chitons, clams, snails, tooth shells, cuttlefishes, etc.

monocotyledon (mon′ o kot′ i lē′ dun). A flowering plant belonging to the group in which there is a single cotyledon or seed leaf and in which, as a rule, the leaves are parallel-veined and the flower parts are in threes or in multiples of three.

monoecious (mon ē′ shus). Having both male and female reproductive organs in the same individual. Usually applied to plants.

monohybrid (mon o hī′ brid). An individual (or generation) that is heterozygous in respect to a single pair of allelic genes.

monophyletic (mon′ o fi lĕt′ ik). Of or pertaining to a single stock; a group of forms developed from a single common parent form.

monosaccharide (mon o sak′ a rīd′). A simple sugar, not decomposable by hydrolysis; glucose ($C_6H_{12}O_6$) is an example.

Monotremata (mon o trē′ mă ta). Egg-laying mammals having a cloaca; the duckbill (Platypus) and spiny anteater (Echidna) of Australia are the only surviving types.

morphology (mor fol′ o ji). That branch of biology dealing with the form and structure of animals and plants.

mosasaur (mō′ sa sawr). Huge extinct marine lizards (Mosasauria, belonging to the reptilian group Diapsida), which had a long, powerful, flattened swimming tail and limbs shortened and modified into paddles. These "sea serpents" were numerous during the Cretaceous period.

moss. A plant belonging to the higher of the two subdivisions of the bryophytes, characterized by the small, leafy, often tufted stems of the gametophyte generation, bearing sex organs at the tips and producing a leafless parasitic sporophyte generation in the form of a stalked, spore-producing capsule arising from the tip of the gametophytic plant.

motor neuron. A nerve cell that carries stimuli to muscles, causing them to contract, or to glands, causing them to secrete.

mucosa (mū kō′ sa). A membrane lining the cavities and tubes communicating with the surface of the vertebrate body, and secreting a mucous fluid.

mucous (mū′ kus). A viscid, slippery secretion produced by mucous membranes, which it moistens and protects.

multiple allelomorphs. Three or more different genes that bear an allelomorphic relationship to each other.

multiple fission. The division of the parent organism into many minute masses consisting of cytoplasm and nucleus, each mass capable of growing into a full-sized individual, as in some types of sporulation; *cf. binary fission.*

mutation (mū tā′shun). The appearance of a new character that is due to a change in a gene.

myelencephalon (mī′e len sef′a lon). The fifth and most posterior of the five major divisions of the vertebrate brain, lying between the metencephalon and spinal cord; the medulla oblongata.

myelin (mī′e lin). A semifluid, fatty substance that forms a sheath around certain nerve fibers.

Myriapoda (mir i ap′o da). A "class" of Arthropoda having tracheae, one pair of antennae, and many unspecialized legs; centipedes, millipedes, and certain other types. (According to modern views, this convenient grouping is actually an artificial one, at least four true classes being included.)

nautiloid (naw′ti loid). A cephalopod mollusk belonging to a group characterized by having an external, chambered shell, either straight or variously curved or coiled, with straight or simply bent sutures where the partitions meet the outer shell. The group was important in the Ordovician and Silurian, but only the genus Nautilus now survives.

nematocyst (nem′a tō sist). One of the stinging structures characteristic of Hydra and other coelenterates; they are usually poison-filled capsules containing coiled, ejectable hollow stinging "threads" and are formed within specialized cells.

nephridium (ne frid′i um). An excretory organ of certain invertebrate animals (worms, mollusks, etc.) corresponding approximately in function to the kidney of vertebrates. It is commonly a coiled tube with a funnellike inner end, leading from the coelom to the exterior, as in the earthworm; *cf. nephrostome.*

nephrostome (nef′ro stōm). The funnellike opening at the inner end of a nephridium, as in the earthworm. Also an opening (originally like that in the earthworm) connecting the coelom with the uriniferous tubules of the kidney in certain Amphibia.

nerve center. A cluster of cell bodies of efferent neurons. A group of associated nerve cells controlling those impulses concerned with or regulating any bodily function.

nerve impulse. A chemicophysical change in a nerve fiber, induced by stimulation, which travels along the fiber.

nerve net. A network of primitive nerve cells, each of which appears continuous with one or several adjacent cells without intervening synapses. An example of this type of nervous system is found in Hydra.

nervous tissue. Tissue, made up of nerve cells, capable of transmitting impulses, as the tissues of the brain, spinal cord, and nerves.

neural canal (nū′ral). The opening in a vertebra through which the spinal cord extends; enclosed dorsally by the neural arch and ventrally by the centrum.

neural spine. A projection rising from the middle of the neural arch of a vertebra.

neural tube. The ectodermal tube formed beneath the surface ectoderm of a chordate embryo by the union of the neural folds along their crests or by a modification of this process; the forerunner of the brain and spinal cord.

neuromotor apparatus (nū ro mō′ter). In more complex Protozoa, a group of protoplasmic fibrils leading from ciliated regions to zones of specially contractile protoplasm.

neuron (nū′ ron). A nerve cell.

nicotinic acid (nik o tēn′ ik). Vitamin B_6. Its absence from the diet leads to pellagra.

nitrogenous wastes (nī′ trŏj′ e nus). A heterogenous mixture of nitrogen-containing wastes, produced as a result of protein metabolism.

node. One of the places upon a stem that normally bears a leaf or whorl of leaves and an axillary bud or buds from which branch shoots may arise.

notochord (nō′ tō kord). A cylindrical stiffening rod of cells beneath the nervous system of a chordate embryo (also present in the adult in some lower chordates). A characteristic structure of the Chordata, it is the forerunner of the spinal column of the vertebrate animals.

nucleolus (nu klē′ o lus). A small, usually rounded body frequently found in the cell nucleus, of different chemical composition from the rest of the nucleus. Its function is uncertain.

nucleus (nu′ klē us). A highly refractive, deeply staining body of specialized protoplasm found within nearly all cells; it contains the chromatin of the cell and appears to regulate various cell processes.

nuclear membrane. A thin film of differentiated protoplasm surrounding the nucleus of a cell.

nuclear sap (nu′ klē ar). A clear fluid that fills all parts of the nucleus not occupied by other structures

occipital condyle (ok sip′ i tal kon′ dīl). An articular surface on the occipital bone, by which the skull articulates with the atlas (first vertebra).

olfactory (ol fak′ tō ri). Pertaining to the sense of smell.

olfactory lobe. A lobe of the brain projecting forward from the anterior lower part of each cerebral hemisphere.

ontogeny (on toj′ e ni). The life history or development of an individual organism.

oögenesis (ō ō jen′ e sis). The series of changes undergone by female germ cells in preparation for reproduction, resulting in the production of a mature egg and three polar bodies from each primary oocyte.

oögonium (ō ō gō′ ni um). One of the early germ cells of a female animal, prior to the beginning of oögenesis.

open vascular bundle. A vascular bundle containing cambium between the xylem and phloem and thus capable of secondary increase in thickness.

optic nerve (op′ tik). The special nerve of sight, connecting the eye and the optic centers of the brain.

order (taxonomic). A group of animals forming a subdivision of a class, composed of one or more families.

organ. A group of cells or tissues performing some specific function.

organic. Consisting of or containing organs. Pertaining to or derived from living organisms; exhibiting characters peculiar to living organisms.

organism. A living being, whether plant or animal.

origin (morphologic). The more fixed, central, or larger attachment or end of a muscle; *cf. insertion.*

Ornithischia (or ni this′ ki a). One of the two dinosaur stocks, characterized (in part) by a four-pronged pelvis.

osmosis (oz mō′ sis). The passage of a solvent through a semipermeable membrane, from a region of lower concentration to one of higher concentration of the solute.

osmotic pressure (os mŏt′ ik). The unbalanced pressure due to molecular activity, which gives rise to the phenomena of diffusion and osmosis, as in a solution in which there are differences of concentration.

ovarian follicle (o var′ i an fol′ i kl). A structure formed in the vertebrate ovary by a group of specialized soma cells that surrounds and nourishes the developing germ cell.

ovary (ō′ va ri). A female reproductive organ in which eggs (ova) are produced.

oviduct (ō′ vi dukt). A tube or duct serving exclusively or especially for the passage of the eggs from the ovary to the exterior or to some part communicating with the exterior.

oviparous (ō vip′ a rus). Producing eggs that hatch after being extruded from the body.

ovoviviparous (ō′ vo vi vip′ a rus). Producing young from eggs that are retained in the oviduct during their development but without attachment to the oviduct; the developing embryo obtains its nourishment wholly from food material stored within the egg.

ovulation (ō vū lā′ shun). The act of producing eggs or ovules or the act of discharging them from an ovary.

ovum (ō′ vum). An egg; a relatively large, passive cell that, in preparation for reproduction, has undergone one or two unequal divisions; see *meiosis*, *maturation*, *polar bodies*.

oxidation (ok si dā′ shun). The chemical process of combining with oxygen.

oxyhemoglobin (ok′ si hē′ mo glō′ bin). Hemoglobin in loose combination with oxygen.

palate (pal′ at). The roof of the mouth, consisting of the structures that separate the mouth from the nasal cavity

paleontology (pā′ li on tol′ o ji). The science that deals with the life of the past geological periods.

palisade parenchyma (pal i sād′ pa reng′ ki ma). In plants, a tissue composed of columnar cells containing chloroplasts, situated immediately below the upper epidermis of many foliage leaves.

pancreas (pan′ kri as). A gland that secretes a fluid containing several digestive enzymes, discharging into the intestine. It also secretes the hormone insulin.

Paramecium (par a mē′ si um). A genus of elongated, ciliated fresh-water Protozoa.

parasite (par′ a sīt). An organism that lives in or on another species of organism (its host) at the expense of the latter.

parathromone (par a thrō′ mōn). The hormone secreted by the parathyroid glands.

parathyroid gland (par a thī′ roid). One of four small endocrine glands that are attached to or imbedded in the thyroid. They are thought to regulate the calcium metabolism of the body.

parenchyma (pa reng′ ki ma). In higher plants, a relatively unspecialized tissue composed of living, thin-walled cells that have the diameters essentially equal and remain capable of cell division after maturity.

parthenogenesis (par′ then o jen′ e sis). The development of an egg without fertilization.

pectoral girdle (pek′ tor al). A group of connected bones serving to attach the bones of the forelimbs of vertebrate animals to the rest of the skeleton.

pedicel (ped′ i sel). Any slender stalk; in plants, the stems that bear the individual flowers of a cluster.

peduncle (pē dung′ kl). A primary flower stalk, supporting either a cluster or a solitary flower.

pelvic girdle (pel′ vik). A group of bones serving to join the bones of the hind limbs of vertebrate animals to the rest of the skeleton.

pentadactyl limb (pen′ ta dak′ til). The typical limb of terrestrial vertebrates, having five digits in the hand or foot, a group of small wrist or ankle bones, two long bones in the forearm or shin, and a single long bone in the upper arm or thigh.

pepsin (pep′ sin). An enzyme of the stomach of vertebrate animals, whose function is digestion of many kinds of protein.

pepsinogen (pep sin′ o jen). An inactive precursor substance from which the enzyme pepsin is formed by the action of the hydrochloric acid in the stomach.

peptones (pep′ tōnz). Intermediate products formed in the breakdown of proteins to amino acids during the process of digestion.

perennial (per en′ i al). Continuing to live from year to year.

perfect flower. A flower possessing the essential parts (male and female organs), whether or not it has petals and sepals.

pericardium (per ĭ kar′ di um). The membranous sac enclosing the heart.

pericycle (per′ i sī kl). In vascular plants, a thin layer of fibrous and parenchymous tissue dividing the cortex from the central region in stems and roots; the outermost layer of the stele.

period. A division of geologic time longer than an epoch and included in an era.

peripheral nervous system (per if′ er al). All nerve tissue lying outside the brain and spinal cord.

Perissodactyla (per′ is so dak′ ti la). Ungulate mammals with the major axis of the foot passing through the middle toe; the "odd-toed" ungulates, including horses, rhinoceroses, etc.

peristaltic (per i stal′ tik). Designating, or pertaining to, the peculiar wormlike wave motion of the intestines and other hollow muscular structures, produced by the successive contraction of the muscular fibers of their walls, forcing their contents onward.

peritoneum (per i tō nē′ um). The membrane covering the viscera and lining the coelomic cavity in many animals; in mammals, restricted to the abdominal cavity.

permeable (per′ mē ă bl). Capable of being permeated; passable; penetrable; used especially of substances that allow the passage of fluids.

petal. One of the divisions of a corolla; a floral leaf belonging to the cycle or cycles between the calyx and the stamens; often brightly colored.

petiole (pĕt′ ĭ ole). The slender stalk that supports the blade of a foliage leaf.

petrifaction (pet rĭ fak′ shun). A method of fossilization by molecular replacement of the original substance by a mineral substance, commonly silica.

phagocyte (fag′ ō sīt). Any white blood cell that shows special activity in ingesting and destroying waste and harmful material in the blood or tissues of the body; an "eating" cell.

pharynx (far′ inks). The part of the alimentary canal between the cavity of the mouth and the esophagus. In vertebrates, the portion of the digestive tract at the back of the mouth into which the gill clefts open.

phloem (flō′ em). One of the conductive tissues in vascular plants. It serves for the protoplasmic conduction of dissolved minerals and food materials, and consists typically of sieve tubes and companion cells and usually, in addition, various kinds of parenchyma and fiber cells, stone cells, etc.

photosynthesis (fō′ tō sinth′ e sis). The construction of carbohydrates from carbon dioxide and water by the energy of sunlight in the presence of chlorophyll.

phylogeny (fī loj′ e ni). The racial history of an animal or plant type; the evolution of a race or genetically related group of organisms (as a species, family, or order), in distinction from ontogeny.

phylum (fī′lum). One of a dozen or more major groups into which the animal kingdom is divided; in general, the largest group of which it can be said that the members are clearly related. Sometimes applied to plants.

physiology (fiz′i ol′ o ji). The branch of biology that deals with the functions of animals and plants and the processes going on in them.

pia mater (pī′ a mā′ ter). The delicate and highly vascular membrane of connective tissue investing the brain and spinal cord, internal to the arachnoid and dura mater.

pineal body (pĭn′i al). A structure on the dorsal side of the brain in vertebrate animals. It is homologous with the pineal eye, and may have endocrine functions.

pineal eye. In the head of larval lampreys and some reptiles, a body raised on a stalk from the brain, bringing it near the upper surface of the head in the median line, and having the structure of an eye, with a more or less distinct retina and lens; homologous with the pineal body of other vertebrates.

pioneer community. A community or society made up of organisms that are tolerant of extreme physical conditions and that are among the first to occupy newly available living places.

pistil (pis′ til). The ovule-bearing organ of a seed plant; the ovary with its appendages.

pistillate flower (pis′ tĭ lāt). A flower having pistils but no stamens.

pith. In dicotyledonous plants, the loose spongy tissue commonly occupying the center of the stem within the vascular cylinder.

pitocin (pĭt ō′ sin). One of the hormones secreted by the posterior lobe of the pituitary body.

pitressin (pĭt res′ sin). One of the hormones secreted by the posterior lobe of the pituitary body.

pituitary body (pĭ tū′ i ta ri). A glandular endocrine organ beneath the brain, composed in part of nervous tissue.

pivot joint. A joint with a rotary movement in one plane.

placenta (pla sen′ ta). In viviparous mammals, a vascular tissue dovetailing into the wall of the uterus on one side and connected with the umbilical cord on the other, thus forming an intimate nutritive connection between the embryo and the mother.

Placentalia (plas en tā′ li a). A subclass or division of mammals including all except the monotremes and marsupials.

Planaria (pla nar′ i a). A genus of free-living fresh-water flatworms.

plasma (plas′ ma). The liquid part of the blood.

plastid (plas′ tid). One of several kinds of cytoplasmic bodies in cells, such as the green bodies in plant cells, which are centers of chemical activity.

platelet. Small disk-shaped, biconvex bodies in the blood, of uncertain origin, which play a part in causing blood to clot.

Platyrrhini (plat i rī′ nē). A division of Primates including the American monkeys, as distinguished from the Old World apes and monkeys (Catarrhini).

plesiosaur (plē′ si o sawr′). One of the Mesozoic marine reptiles of the group Synaptosauria, having a broad, flattened trunk with paddlelike forelimbs and hind limbs and more or less elongated neck and tail.

pleura (ploor′ a). The thin delicate membrane that lines each half of the thoracic cavity of mammals and is reflected over the surface of the lung of the same side.

plumule (ploo′ mūl). The embryonic leaf shoot.

polar body. A small nonfunctional cell; that one of the two cells produced by each division in oögenesis which receives almost no cytoplasm.

pollen (pol′ en). The fertilizing grains contained in the anther.

pollination (pol i nā′ shun). The transfer of pollen from the anther to the stigma.

polyp (pol′ ip). One of the feeding individuals of a colonial hydroid or coral colony (Coelenterata) or simple related forms; tubular, sessile, or stalked, usually provided with tentacles.

polypeptid (pol i pep′ tid). An intermediate product formed in the breakdown of proteins during the process of digestion.

polysaccharide (pol i sak′ a rīd). Any carbohydrate decomposable by hydrolysis into more than two molecules of simple sugars.

pons. A part of the brain stem that acts as a bridge uniting the two halves of the cerebellum and as a bridge between the medulla and the cerebrum; a part of the metencephalon.

portal system. A blood vessel or group of vessels beginning and ending in capillaries; *cf. hepatic portal vein.*

posterior (pos tēr′ i or). At or toward the hinder end of the body; caudal.

postganglionic neuron (post′ gang gli on′ ik noo′ ron). A visceral motor nerve cell whose axon transmits impulses to the appropriate end organ, visceral muscle, or gland, as the case may be.

precipitin (prē sip′ i tin). A substance (antibody) contained in the blood that produces a precipitate when it encounters its specific protein antigen in blood serum or other solution.

precocious (prē kō′ shus). Exceptionally early in development; prematurely developed.

preganglionic (prē′ gang gli on′ ik). An efferent nerve fiber (usually medullated) arising from a cell body in the central nervous system and terminating in an autonomic ganglion.

premolar tooth. A mammalian tooth situated in front of the true molars (between them and the canines when the latter are present).

primary oöcyte (ō′ ō sīt). A female germ cell during the growth period and prior to the first maturation division.

primary spermatocyte (sper′ ma tō sīt). A male germ cell during the growth period and prior to the first maturation division.

Primate (prī′ māt). A mammal of the order that includes man, the apes, and apelike animals, monkeys, tarsioids, and lemurs.

prophase (prō′ fāz). Any early stage of mitotic cell division prior to the equatorial plate stage.

prostate gland (prŏs′ tāt). A glandular body that surrounds the commencement of the male urethra in mammals, discharging by ducts opening into the urethra.

protease (prō′ tē ās). One of the enzymes that converts proteins into amino acids.

proteose (prō′ tē ōs). An intermediate product formed in the breakdown of proteins to amino acids during the process of digestion.

proteins (prō′ tē in). Various nitrogenous compounds formed by the union of two or more amino acids.

prothallus (prō thal′ us). The gametophyte plant of the Pteridophyta.

prothrombin (prō throm′ bin). The material from which thrombin is formed in the process of blood clotting.

Protista (prō tis′ ta). The unicellular organisms collectively, including both Protozoa and unicellular Thallophyta.

protonephridial system (prō′ tō ne frid′ i al). A primitive excretory system consisting of flame cells and connecting tubes. This system is characteristic of the flatworms.

Protophyta (prō tof′ i ta). The more plantlike Protista, containing chlorophyll.

protoplasm. The living matter of which animals and plants are essentially composed.

Protozoa (prō tō zō′ a). One-celled animals. The phylum comprising the one-celled animals, including colonial forms in which the cells of the colony are, at least potentially, all alike.

proximal (prok′ si mal). Next to, or toward, the point of attachment.

Pteridophyta (ter i dof′ i ta). A phylum of plants that includes the ferns and fern allies.

ptyalin (tī′ a lin). The starch-digesting enzyme of the saliva.

pubis (pū′ bis). The anterior one of the two ventrally placed bones in the pelvic girdle of Amphibia and all higher vertebrates.

pulmonary artery (pul′ mon er i). An artery that conducts venous blood from the heart to the lungs.

pupa (pū′ pa). A quiescent stage in the development of an insect, just before the adult condition is reached, during which the larval characteristics are metamorphosed into those of the adult.

pyloric valve (pī lōr′ ik). A ring of circularly disposed muscle fibers forming a sphincter valve at the opening from the stomach into the small intestine.

Quaternary (kwa ter′ na ri). The latest division of geologic time; the Pleistocene epoch.

race. A group of individuals having certain characteristics in common because of common ancestry. Used sometimes, as in man, for a major subdivision of a species; sometimes, in a more general sense, to include all the forms of some branch of the animal or plant kingdom.

radial symmetry. An arrangement of the parts of an object or organism such that it is capable of being divided into halves that are mirrored images of one another, by two or more planes, all of which pass through a common longitudinal axis.

radicle (rad′ i kl). The embryonic root of a seed plant.

ramus (rā′ mus). A branch; one of the branches of a spinal nerve.

ramus communicans (rā′ mus ko mū′ ni kans). That one of the branches of a spinal nerve that supplies the visceral organs. A bundle of nerve fibers connecting autonomic ganglia with a spinal nerve.

recapitulation (rē′ ka pit′ ū lā′ shun). The repetition of ancestral stages during the development of the individual.

Recent (geological). The period of time, amounting to some 20 to 25 thousand years, since the retreat of the Pleistocene ice sheets of the latest (Wisconsin or Wurm) glacial stage. In a geological sense the Recent may be no more than the latest of the warm interglacial stages of the Pleistocene epoch.

receptacle (rē sep′ ta kl). The more or less expanded or produced portion of a plant axis that bears the organs of a flower or the collected flowers of a head.

receptor (rē sep′ tor). A cell or group of cells that are especially adapted to receive some particular stimulus; a sense organ.

rectum (rek′ tum). The terminal portion of the large intestine in the higher vertebrates.

red algae (ăl′ jē). Algae of a class characterized by the presence of red or violet pigment in addition to chlorophyll; the Rhodophyceae.

red blood cell. In mammals, a nonmotile, highly differentiated blood cell, lacking a nucleus and containing hemoglobin; in other classes of vertebrates, the cells are nucleated.

reduction division. That one of the two cell divisions in the maturation of germ cells and spores in which the paired chromosomes separate to form two haploid sets of chromosomes; see also *meiosis*.

reflex action. An action performed as a result of an impulse that passes over a reflex arc. It is involuntary and is often performed without the consciousness of the organism.

reflex arc. A group of two or more neurons, one of them sensory, another motor, so connected as to be able to transmit impulses resulting in reflex actions.

regular flower. A type of flower in which there is close resemblance between all the petals and between all the sepals.

relative humidity. The amount of water vapor within a given cubic space in terms of the percentage of saturation.

rennin (ren′ in). A milk-clotting enzyme secreted by the stomach.

respiratory system (re spīr′ a tō ri). A system of organs adapted for the taking in of oxygen and the expulsion of carbon dioxide

retina (ret′ ĭ na). The light-sensitive inner layer of the eye.

reversion. A return toward some ancestral type or condition; the reappearance of an ancestral character or characters.

rhizoid (rī′ zoid). In ferns, mosses, and liverworts, one of the slender rootlike filaments that attach the gametophyte to the substratum and function as absorptive organs.

riboflavin (rē bo flā′ vin). A water-soluble vitamin important for normal growth and in the control of oxidative processes of cells; the same as vitamin B_2 or G.

rods. A type of light-receptor cell in the retina of the eye which is especially sensitive to light but the stimulation of which results in only monochromatic sensations.

root. In higher plants, a portion of the plant body bearing neither leaves nor reproductive organs but provided with an apical growing point and functioning as an organ of absorption, an aerating organ, a food reservoir, or a means of mechanical support.

root cap. The cushion of epidermal tissue covering the apex of most roots, serving to protect the active meristematic cells behind it.

root hair. A hairlike tubular outgrowth of the epidermis found commonly near the apex of a growing rootlet, performing the work of absorption and being continually renewed.

sacrum (sā′ krum). A group of vertebrae, more or less fused, in the region between the hips.

saliva (sal ī′ va). The fluid secreted by the salivary glands and emptied into the mouth. It contains the digestive enzyme ptyalin.

sapwood. The usually lighter, more porous, and younger wood just beneath the bark.

sarcostyle (sar′ kō stīl). One of the elements of a muscle cell. A slender, threadlike strand running from one end of the cell to the other.

Saurischia (sawr ĭs′ kĭ a). One of the two dinosaur stocks, characterized (in part) by a three-pronged pelvis.

sclerenchyma (skler ĕng′ kĭ ma). In higher plants, a tissue composed of cells that have the cell walls thickened and lignified and often mineralized and that are usually without living protoplasm and incapable of further growth when mature.

sclerotic coat (skle rŏt′ ik). The outer white coat of the eyeball.

scrotum (skrō′ tum). The external bag or pouch that contains the testicles of the males in most mammals.

sea lily. One of the stalked types of Echinodermata; the Crinoidea.

sea urchin. An animal belonging to the phylum Echinodermata, having a somewhat globular form and a thin, brittle shell of calcareous plates covered with well-developed spines; the Echinoidea.

sebaceous glands (sē bā′ shus). The oil glands of the skin.

secondary oöcyte (ō′ ō sīt). A female germ cell after the first division of maturation and before the second.

secondary spermatocyte (sper′ mă tō sīt′). A male germ cell after the first division of maturation and before the second.

secrete (sē krēt′). To produce from the blood or other fluids or substances in the protoplasm some new material to be used in metabolism or otherwise.

secretin (sē krē′ tin). A hormone produced in the small intestine that stimulates secretion by the pancreas and liver.

seed. The reproductive structures produced by flowering plants that contain an embryonic sporophyte, capable of developing by germination.

seedfern. A group of Paleozoic plants, the Cycadofilicales, intermediate in structure between cycads and ferns, and the first plants to produce seeds.

self-pollination. Self-fertilization in seed plants; the transfer of the ripe pollen from the anthers to the stigma of the same flower.

semicircular canal. One of three curved tubes forming part of the inner division of the ear in vertebrates and concerned with equilibrium.

seminal vesicle (sĕm′ i nal vĕs′ i kl). A vesicle or sac, variously formed in different animals; connected with the seminal duct, serving for temporary storage of the sperm.

seminiferous tubules (sĕm i nif′ er us). The greatly convoluted tubules that make up most of the bulk of the testes.

sense organ. An organ, as the eye or ear, whose function is to respond to stimulation of a particular kind by occasioning a special kind of sensation.

sensory neuron. A nerve cell that conducts impulses from a sensory receptor into the central nervous system.

sepal (sē′ pal). A leaflet or division of the calyx.

serial homology. Homology between segments of the same organism.

serum. The liquid part of coagulated blood; blood serum; contains specific immune bodies, as antitoxins or agglutinins

sessile (ses′ il). Attached directly, as distinguished from stalked. Sometimes, also, attached, as distinguished from free-living.

sex chromosome. Usually, one or a pair of chromosomes that are not alike in both sexes of the same species, and the distribution of which determines or influences the sex of the individual.

sex linkage. The association of an inherited character with sex, due to the fact that the gene for that character is located in the sex chromosome.

sexual reproduction. Usually refers to reproduction involving the fertilization of an ovum by a spermatozoon; also used for the process of conjugation and fission that occurs in unicellular organisms; and includes unisexual reproduction, or parthenogenesis, in which a new individual is produced by the development of an unfertilized ovum.

sexual selection. The supposed preference by animals of one sex for certain qualities in the other sex, leading to the preservation of these qualities in later generations.

sieve tube (siv tūb). In plants, a phloem tube that consists of an end-to-end series of elongated, thin-walled living cells, sometimes lacking nuclei when mature, with perforated end walls, through the holes in which cytoplasmic strands connect the cytoplasm of adjacent cells; a characteristic feature of phloem tissue.

simple respiration. A type of respiration in which there is a direct exchange through the cell membrane between the protoplasm of the cell and the gases of the external medium.

skeleton (skel′e tun). Relatively hard and rigid protective and supporting structures of an organism.

smooth muscles. Muscles that are composed of spindle-shaped nonstriated fibers, each fiber with a single, elongated nucleus. Smooth muscles are found chiefly in the circulatory, respiratory, digestive, and urinogenital systems.

soft palate (pal′at). A movable fold of mucous membrane enclosing some muscle fibers, suspended from the posterior margin of the hard palate, partially separating the mouth from the pharynx.

soma (sō′ma). The body of a metazoan, exclusive of the germ cells.

somatotropic hormone (sō′ma tō trŏp′ ik). The growth hormone of the anterior lobe of the pituitary body.

somite (sō′mīt). One of the segments into which the bodies of annelids, arthropods, and chordates are divided.

species (spē′shēz; spelled and pronounced alike in singular and plural). A group of closely similar individuals that, in general, are alike in most morphological and physiological characters, produce fertile offspring, and have a common ancestry.

specific heat. The amount of heat required to raise the temperature of 1 gram of water 1°C. (from an initial temperature of 15° to a final temperature of 16°C.).

spermatid (sper′ma tid). One of the cells that arise by division of the secondary spermatocytes and that change into spermatozoa.

spermatogenesis (sper′ma tō jen′ e sis). The ripening of male germ cells, ending in the production of spermatozoa.

spermatogonium (sper′mă tō gō′ ni um). One of the primordial germ cells of a male animal during the periods of multiplication and growth and prior to the beginning of spermatogenesis.

spermatophore (sper′ mă tō fōr′). A special capsule, packet, or mass, enclosing a number of spermatozoa, extruded by a male animal and either transferred directly into the female genital chamber by the male or deposited to be picked up later by the female.

Spermatophyta (sper′ma tof′ i ta). A phylum embracing the highest plants—those that produce seeds; the seed plants or flowering plants.

spermatozoön (sper′ma tō zō′ on); plural, **spermatozoa.** A male germ cell or sperm cell of an animal, equivalent to the microgamete in plants; its function is the fertilization of the egg.

spherical symmetry. The symmetry of a ball, any section through the center dividing the organism into symmetrical or mirrored halves.

sphincter muscle (sfingk′ter). A ringlike muscle surrounding, and able to contract or close, a natural opening or passage.

spicule (spĭk′yūl). One of the variously shaped siliceous or calcareous supporting structures that make up part or all of the skeleton of a sponge; commonly needle-shaped or radiate.

spinal cord. That part of the central nervous system of a vertebrate lying behind the brain and largely enclosed by the vertebrae.

spinal nerves. The pairs of nerves that leave the spinal cord and, passing out between the vertebrae, supply the muscles and skin of the trunk and limbs and connect with the nerves of the sympathetic or autonomic system.

spindle fibers. Cell structures resembling threads, grouped in the form of a spindle or double cone. They are formed in the cytoplasm of a cell during mitosis.

spireme (spī′rēm). A coiled or tangled thread formed by the chromatin of a cell in the early stages of mitosis.

splint bone. One of the rudimentary, splintlike metacarpal or metatarsal bones on either side of the cannon bone in the limbs of the horse and allied animals.

spongy parenchyma (pa reng′ki ma). In plants, the lower and thicker layer of the mesophyll, consisting of a mass of thin-walled, loosely arranged cells enclosing abundant air spaces.

sporangium (spo ran′jĭ um). The sac or receptacle within which asexual spores are produced.

spore. A small reproductive body, typically unicellular, produced by plants and some protozoans. The spore produced by the sporophyte generation is a haploid cell formed by reduction division of a spore mother cell.

sporophyte (spō′rō fīt). The diploid generation of plants that produces haploid spores by maturation.

stamen. That organ of the flower giving rise to the male gametes.

staminate flower (stăm′i nāt). A flower having stamens but no pistils.

stapes (stā′pēz). The innermost of the chain of small bones in the ear of mammals.

starch. A white, odorless, tasteless, and insoluble, granular or powdery polysaccharide carbohydrate. The form in which most plants store carbohydrates.

steapsin (stē ap′sin). The fat-splitting enzyme of the pancreatic fluid.

stegocephalian (steg′ ō sē fā′ li an). A member of an extinct order of crocodile- or salamanderlike, tailed amphibians, with a completely roofed-over skull, and usually having well-developed limbs with four or five digits. They lived during late Paleozoic and early Mesozoic times.

stele (stē′lē). The central cylinder in the stems and roots of vascular plants.

sternum. The breastbone; present in most vertebrates except the fishes and some reptiles.

stigma. That part of the pistil of a flower which receives the pollen grains, and on which the latter germinate.

stipule (stip′ūl). One of the pair of appendages borne at the base of the leaf in many plants

stomata (stō′ma ta). Minute orifices in the epidermis of leaves, stems, etc., through which gaseous interchange is effected.

style. The usually attenuated portion of the pistil connecting the stigma and the ovary.

suberin (sū′ber in). A complex fatty or waxy substance that constitutes the basis of cork.

submucosa (sub′mū kō′ sa). The layer of connective tissue directly under a mucous membrane.

succession. The more or less orderly progression of different types and kinds of biotic communities that, in the course of time, come to occupy any given local area.

supraorbital ridges (sū′pra or′ bi tal). A prominence on the frontal bone above the eye, caused by the projection of the frontal air sinuses.

surface tension. The tension exhibited by the free surface of liquids measured in dynes per centimeter.

sustentative tissue (sus′ ten tā′ tiv). Tissue that is adapted to provide mechanical support and to bind various other tissues together.

suture (sū′tūr). The line of union or seam in an immovable articulation, like those between the bones of the skull.

symbiosis (sim bī ō′sis). The association of two species of organisms to their mutual benefit.

synapse (sĭn′ aps). The point of contact of two neurons or, alternatively, the passage of a stimulus from an axon to a dendrite.

synapsis (sĭn ap′ sis). Conjugation of pairs of homologous chromosomes; each pair consists of a maternal and paternal member.

tannin. A substance accumulated in the stems of some plants; it imparts an astringent, bitter taste to tissues in which it is deposited.

taste bud. An end organ of taste consisting of an oval group of spindle-shaped cells, enclosed in an envelope of supporting cells arranged like the leaves of a bud.

taxonomy (taks on′ ō mi). The science of the classification of animals or plants.

telencephalon (tel′ en cef′ a lon). The most anterior of the five major divisions of the brain, consisting of the olfactory lobes and the cerebral hemispheres.

telolecithal egg (tĕl′ ō les′ i thal). A type of egg in which the yolk is concentrated toward the vegetative pole.

telophase (tĕl′ ō fāz). The final phase of mitotic cell division, in which the nuclei are reconstructed.

tendon. A tough cord or band of dense, specialized, regularly arranged white connective tissue uniting a muscle with some other part and transmitting the force that the muscle exerts.

Tertiary (tir′ shĭ er i). A term used to include that period of geologic time extending from the beginning of the Cenozoic era up to the Pleistocene.

testis (tes′ tis). A male genital or reproductive organ in which the spermatozoa are produced.

testosterone (tes tos′ ter ōn). A hormone produced by the interstitial cells of the testis.

tetrad. A quadruple body consisting of the four chromatids or "half chromosomes" that are formed from each pair of homologous chromosomes at an early stage in maturation.

Thallophyta (tha lŏf′ i ta). A phylum of plants of very diverse habit and structure, including the algae, bacteria, fungi, and lichens, and in some classifications also the slime molds.

thallus (thal′ us). The plant body characteristic of the thallophytes, showing no differentiation into distinct members, as stems, leaves, and roots, or composed of members resembling, but not homologous with, those of the higher plants.

thiamin (thī′ ăm in). Vitamin B_1.

thigmotropism (thig mŏt′ rō pizm). An orientation of an organism in response to contact.

thoracic cavity (tho ras′ ik). The cavity of the thorax or chest.

thrombin (throm′ bin). A substance present in serum that unites with fibrinogen to form fibrin.

thrombokinase (throm′ bō kin′ ās). A substance present in the tissues which accelerates the clotting of the blood, presumably by converting prothrombin, in the presence of calcium salts, into thrombin.

thymus (thī mus). One of the endocrine glands located in the thoracic cavity above the heart. It is thought that this gland is associated with sexual development.

thyroid gland (thī′ roid). One of the endocrine glands that is situated in the neck.

thyrotropic (thī rō trōp′ ik). Stimulating the thyroid gland and causing it to produce thyroxine.

thyroxin (thī rok′ sin). A hormone produced by the thyroid gland that regulates metabolic activity.

tissue. A group of cells of similar structure forming a continuous mass or layer.

trachea (trā′kē a). A tube. The tube conveying air to and from the lungs in vertebrates. One of the air tubes of an insect In plants, elongated tubular cells arranged in series to form water-conducting vessels of the xylem.

tracheid (trā′kē id). In plants, a long tubelike cell peculiar to xylem, characterized by tapering, closed ends and by thickened, strongly lignified walls commonly having bordered pits.

transpiration (tran′spĭ rā′shun). Water loss by plants; the emission or exhalation of water vapor from the surface of green tissues in plants.

trilobite (trī′lō bīt). An extinct group of marine Crustacea that persisted throughout the Paleozoic and was a dominant group in the early part of that era.

triploblastic (trip lō blas′tik). A body or structure comprising ectoderm, entoderm, and mesoderm.

tropism (trō′pizm). An orientation of an organism with reference to a stimulus; a turning toward or away from; also called *taxis.*

trypsin (trip′sin). An enzyme, secreted by the pancreas, that acts on proteins.

trypsinogen (trip sin′ō jen). The inactive substance from which the enzyme trypsin is produced.

turgor (tur′gor). Distension due to some internal agent or expansive force; the state of normal turgidness and tension in living cells

tympanic membrane (tim pan′ik). A thin membrane forming the external boundary of the middle ear; the eardrum.

Ungulata (ung gū lā′ta). The taxonomic group comprising the hoofed mammals.

uniformitarianism. The doctrine that geological processes of the past were similar to those of the present time.

uniovular twins. Twins that develop from a single egg; identical twins.

unisexual reproduction. Parthenogenesis; the development of an egg without fertilization.

ureter (ū rē′ter). A tube conducting urine away from the kidney.

urethra (ū rē′thra). The duct by which urine is discharged from the bladder.

urinary bladder (ū′ri ner′i). A distensible membranous sac, serving for the temporary retention of the urine.

urine. In mammals, a fluid excretion from the kidneys. Most of its elements are waste products of body metabolism or products derived from food.

urogenital sinus (u′ro jen′i tal sī′nus). That portion of the body of the female by which the vagina and urethra communicate with the exterior.

uterus (ū′te rus). A modified portion of the oviduct in which the eggs undergo at least part of their development. Strictly, the term *uterus* is applicable only in animals in which the developing embryo becomes attached to the wall of the organ.

vacuole (vak′ū ōl). A region within a cell occupied by a liquid other than protoplasm, usually water with various substances in solution.

vagina (va jī′na). In female mammals, a canal that leads from the uterus to the external orifice of the genital canal or to the cloaca; extended also to a canal of similar function or location in various other animals.

vagus (vā′gus). The tenth cranial nerve.

variation. Divergence in structural or physiological characters.

vas deferens (vas def′e rĕnz). A duct conveying spermatozoa from the testis to the exterior.

vascular system. In plants, the aggregate of the conductive tissues; in animals, the circulatory system.

vegetative pole. The part of an egg diametrically opposed to the animal pole; in all telolecithal eggs, it is marked by a concentration of yolk.

vegetative reproduction. Reproduction, or propagation, by nonsexual processes.

vein. A vessel conveying toward the heart blood that has already traversed capillaries since leaving the heart. Also, one of the vascular bundles forming the framework of fibrous tissue of a leaf.

venation. In plants, the arrangement and disposition of the veins or vascular bundles in the green tissue of a leaf blade.

ventral. Literally, pertaining to the belly; opposite the back.

ventral ramus. That one of the branches of a spinal nerve which innervates the skin and muscles of the appendages and of the lateral and ventral parts of the body wall.

ventral root. The ventral one of the two roots by which a spinal nerve is connected with the spinal cord.

ventricle, of brain (ven′tri kl). One of the systems of communicating cavities that are continuous with the central canal of the spinal cord.

ventricle, of heart. The posterior chamber of the heart in fishes, Amphibia, and some reptiles and one of the two posterior chambers in higher vertebrates. Its function is the propulsion of the blood through the circulatory system.

vertebra (vur′ te bră). One of the bony or more or less cartilaginous segments composing the spinal column or backbone.

vertebrate (vur′ te brāt). Having a backbone or spinal column; also, of, or pertaining to, the Vertebrata.

viscera (vis′er a). The organs contained within the body cavity; applied chiefly to the organs of the abdomen.

vitamin (vī′ta mĭn). One of the group of organic substances, exclusive of the energy-producing foods, that are necessary for proper metabolism in animals.

vitreous humor (vit rē us). The clear, colorless, transparent jelly that fills the posterior chamber of the eyeball.

viviparous (vī vip′a rus). Giving birth to living young that have been nourished within the body of the mother.

Volvox (vol′ voks). A small spherical organism composed of flagellated green cells embedded in jelly and arranged in a single layer around a water-filled interior cavity. Sometimes regarded as an animal, though more properly included among plants.

water-vascular system. A system of vessels in echinoderms, containing a circulating watery fluid, used for the movement of the tube feet.

white blood cell. Colorless corpuscles found in the blood. They are true cells with a nucleus and cytoplasm.

white matter. White nervous tissue of the brain and spinal cord that consists largely of myelinated nerve fibers.

xylem (zī′lem). A complex tissue of higher plants, consisting typically of tracheids or tracheae (or both) and usually also of various kinds of wood fibers and parenchyma cells.

yolk. Highly nutritive material, very rich in fats, that is found in most types of eggs.

yolk sac. A more or less spherical membranous sac developed about the yolk by the embryo; formed by the embryos of most vertebrates and cephalopods.

zygote (zī′ gōt). A fertilized egg; a cell formed by the union of two gametes.

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